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Megaherbivores

The influence of very large body size on ecology

R. NORMAN OWEN-SMITH
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'Hints for an agenda: How big is it and how fast does it happen?'
(G. Evelyn Hutchinson 1975)

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Preface

Like the animals it describes, this book has had a long gestation. It started as a Ph.D. thesis on the white rhinoceros, grew into a monograph on rhinoceroses, expanded to include other similarly large herbivores, and then settled on the focus adopted in the pages that follow: the consequences of large size for the ecology of animals such as elephants, rhinoceroses and hippopotami, and by implication extinct species of similar size.

I hope that this work will be of interest to a variety of readers. Firstly, it is written for biologists interested in allometric scaling effects on ecological processes. The correlates of a body mass at the upper limit of the size range among mammalian herbivores are analyzed at various levels, including ecophysiology, behavioral ecology, demography, community interactions and ecosystem processes. Secondly, the book should be an aid to professional conservationists and wildlife managers concerned about the future survival of such large mammals. Scientific facts about these species must be given due cognizance if management actions are to achieve their desired objectives. Thirdly, it is directed towards paleobiologists interested in the ecological roles that similarly large mammals played in the faunas and ecosystems of the past. In particular potential causes of the extinctions of the so-called megafauna during the late Pleistocene are assessed. Finally, I hope that this book will be illuminating to all those who have marvelled at the ways of living of these largest among land animals, whether in the wild or on film. The features of their ecology and behavior are compared and contrasted with those of lesser ungulates.

I owe many debts of gratitude to people who have contributed help or ideas at various stages of the life history of this manuscript. It was a suggestion made by George A. Petrides, then Visiting Professor of Wildlife Management at the University of Pretoria, that first drew me into a study of the white rhinoceros. Rudolf C. Bigalke, then Principal Research Officer of the Natal Parks Board, made the study possible by organizing a temporary position for me with his organization, and by giving me free reign to delve into the social life of white rhinos. John T. Emlen, my doctoral supervisor at the University of Wisconsin, provided much inspiration and support both during the fieldwork period and over the subsequent period of thesis writing far from these animals and their environment. The impetus to delve into allometry was sparked by a conversation with Fred L. Bunnell at the University of British Columbia. R. Dale Guthrie of the University of Alaska opened my mind to the full richness of the large mammal fauna of the far north during the Pleistocene, and the intertwined puzzle of its disappearance.

Many personnel of the Natal Parks Board provided practical assistance. John Vincent saw to my needs during the initial six months, and arranged the aerial counts. Peter Hitchins developed the techniques used for installing radio transmitters on the rhinos, and generously provided much data on black rhinos. Greig Stewart initiated me into the vegetation of the area; Brian Downing and Orty Borquin helped identify many plants, and later Roger Porter provided further botanical assistance. Michael Keep provided veterinary assistance with post-mortems and rhino capture. Aid in catching the rhinos required for marking was provided by John Daniel, Ken Rochat, Mark Astrupp and Brian Thring. Park Wardens Ian Player, Nick Steele and Gordon Bailey helped in many ways, and imparted their wilderness ideals. Several of these people, and also Graham Root, assisted with aerial counts. Bob Crass and later Don Stewart provided valuable support from head office. David Rowe-Rowe organized the printing of photographs. Dawn Denyer saw to it that my grocery book went out each week. Mqhoyi Nkosi carried my equipment and imparted his bush knowledge, while later his son Bheki served as a keen and unobtrusive field assistant.

The book developed its final form under the helpful guidance of various editors and reviewers, including Norman Myers, Tim Clutton-Brock, Robin Dunbar, Robin Pellew and Martin Walters. Special thanks are due to Thomas Foose, for permission to quote extensively from his unpublished thesis, and to Richard Bell, for his vast generosity with comments and ideas on many sections of the book. A number of people provided information or helpful comments on various sections of the manuscript, including D.G. Ashton, Esmond Bradley Martin, Martin Brooks, Graeme Caughley, Johan du Toit, Peter Goodman, Russell Graham, Hans Grobler, Dale Guthrie, Andrew Hansen, Peter Hitchins, Andrew Laurie, Chris Lightfoot, Hanne Lindemann, Paul Martin, Thys Mostert and my wife Margaret Loffell.

The numerous illustrations were patiently drawn by Cheryl Hughes, John Dallman, Cherry Allan, Carol Cardoso and Jenni Saley. Phillip Prim assisted with photographic work. Carol Sam helped with part of the typing, while my own fingers did the rest.

The white rhino study would not have been possible without the financial support provided by the Natal Parks Board, the Wisconsin Alumni Research Foundation, and US National Science Foundation grant no. GB-15304 to John T. Emlen. The Centre for Resource Ecology in the Department of Botany, University of the Witwatersrand, provided the ideal environment within which to develop into their final form the facts and ideas presented in this book.

Norman Owen-Smith
University of the Witwatersrand

1

Prologue

The subjects of this book are the animals that I will designate as megaherbivores. I define this term to include those plant-feeding mammals that typically attain an adult body mass in excess of one megagram, i.e. ten to the power six grams, 1000 kg, or one metric tonne. This demarcating criterion conveniently encompasses elephant, rhinoceros and hippopotamus among living forms, while giraffe slip marginally into the category. Such animals have been colloquially designated pachyderms; but a thick skin is a minor feature, and it is their very large body size that sets these few species apart from the numerous smaller species of unguligrade herbivore that occupy a wide variety of terrestrial ecosystems today. Paleontologists such as Martin (1967) have used the term 'megafauna' to encompass those species attaining a body mass exceeding about 45 kg (100 pounds). However this division is arbitrary and has no functional basis. In this book I show that there are distinctions between animals reaching a mass in excess of 1000 kg, and those of smaller size, in almost all aspects of ecology.

Of course, many whales attain a larger size than any terrestrial mammal, but all whales are carnivorous, feeding on other animals ranging from tiny shrimps to seals. However, among marine mammals there are also the strictly herbivorous sirenians (manatees and dugongs), which feed on submerged plants growing in shallow lagoons and coastal waters. Manatees may weigh up to 1600 kg, while the recently extinct Steller's sea cow weighed up to 6000 kg. I will say little further about these marine megaherbivores in this book, simply because it is difficult to compare their ecology meaningfully with that of terrestrial species, and because I lack familiarity with the literature on marine animals.

The terrestrial megaherbivores extant at the present time are a depauperate remnant of the much greater variety of such forms of animal represented in the faunas of the past until as recently as 11 000 years ago (the end of the Pleistocene). While today elephant, rhino and hippo are found only in Africa and tropical Asia, in previous eras through to the late Pleistocene there were comparably large mammals of a diversity of forms on all continents, occupying a range of ecosystems from arctic steppe and taiga to tropical rain forest and semidesert. During the mesozoic era certain reptilian herbivores (the so-called dinosaurs) attained immense body sizes comparable to or even exceeding those of the largest whales, although it has been suggested that the largest dinosaurs may have been semi-aquatic in their habits. These reptilian megaherbivores all became extinct over a relatively short period at the end of the Cretaceous period, some 100 million years BP. The disappearance of giant mammals from the Americas, Europe and the palearctic region of Asia at the end of the Pleistocene was even more dramatic in its suddenness, and coincided with the spread of humans through these regions.

The continued survival of most of the megaherbivore species currently in existence is somewhat precarious. The large appetites and destructive power of these beasts are incompatible with human agronomic objectives, so that their ranges have become restricted mostly to the island sanctuaries provided by national parks and wildlife reserves. Populations of elephants and rhinos have recently been depleted even within conservation areas, due to illegal hunting stimulated by the high prices fetched by ivory and rhino horn. All three Asian species of rhino are listed by the International Union for the Conservation of Nature as seriously endangered, as also is the Asian elephant. The northern race of the African white rhino is currently on the critical list, while numbers of black rhino and elephant are dwindling rapidly through most of Africa.

However, in African conservation areas where they have been effectively protected, populations of elephant, white rhino and hippo have increased to levels where they have induced vegetation changes that have appeared detrimental not only to their own food resources, but also to habitat conditions for other species of plant and animal. This has led to management intervention in the form of culling operations. These undertakings are controversial because of their interference with ecological processes, and also on humanitarian or animal welfare grounds. We still understand little about how populations of such potentially destructive animals were regulated under pristine conditions.

Thus surviving African species of megaherbivore are embarassingly successful, when protected from human depredation. This raises questions concerning the reasons for the demise of elephants, rhinos and other similarly large beasts from Europe and the Americas at the end of the Pleistocene. The relative importance of climatic change and human predation in these extinctions remains an unresolved problem. What light can the ecology of surviving species of megaherbivore shed on these questions?

What difference has the disappearance of these animals made to the ecosystems that had persisted with megaherbivores as integral constituents until 11 000 years ago? These questions raise some deeper issues with a bearing on the ecological problems now confronting us, *Homo sapiens*, as our populations expand and exert an increasingly strong influence on the functioning of natural ecosystems.

A number of scientific papers, and several books, have appeared recently on the subject of size and scaling in biology. A pioneering recognition of the pervasive importance of body size was by G. E. Hutchinson (1975), as noted in the quotation prefacing this book. During the gestation of the present manuscript, three books have been published focussing specifically on this topic. Peters (1983) documented the pervasive influence of body size on a wide range of physiological and ecological features, from metabolism and locomotion to abundance and productivity. Calder (1984) emphasized underlying dimensional and rate factors, together with aspects of life history. Schmidt-Nielsen's (1984) focus was specifically on aspects of physiology, from heartbeat and metabolic rate to movement and temperature regulation. While Calder's book was restricted largely to birds and mammals, Peters and Schmidt-Nielsen considered the complete range of organisms from protozoa upwards. These books, and other published papers, provide ample evidence that a variety of biological functions are scaled in magnitude or rate in relation to some exponential power of body mass.

In this book the focus is specifically on ecology, although underlying features of nutritional physiology are included. Taxonomic coverage is restricted to ungulates of the orders Perissodactyla and Artiodactyla, together with the subungulates of the order Proboscidea, among extant forms. As large mammalian herbivores these species share a basic ecological unity. The range in body size encompassed spans three orders of magnitude, from the smallest antelope, weighing 4–5 kg, to the largest elephant, weighing over 6000 kg. Geographically I will emphasize the species that share African savanna environments with modern day elephants, rhinos and hippos, since less information is available for Asian ungulates. By restricting coverage to such an ecologically, geographically and taxonomically coherent group of animals, it is possible to delve more deeply into the factors underlying body mass trends than was possible in the wide-ranging reviews cited above. Furthermore this is the group of animals with which I am personally familiar from my own field research. Such first hand contact is an aid in assessing and interpreting the results reported for particular species by other investigators using a variety of techniques.

My doctoral research on the behavioral ecology of the white or square-lipped rhinoceros (*Ceratotherium simum*) provided the initial ideas for this book. The white rhino is in many ways a seminal species. Unlike elephants and other rhinos, it is exclusively a grazer – a habit shared only with hippopotamus among surviving megaherbivores, but with a wider proportion of extinct species. In its grazing habits it has ecological affinities with a variety of bovids and equids that share similar savanna environments in Africa. It thus provides a unique example for unravelling the common influences of very large size on ecology from those deriving from phyletic inheritance or dietary restrictions.

The chapters of this book fall mainly into two kinds. Some review succinctly what is known about the ecology and behavior of living species of megaherbivore. Most of the ecological data from my white rhino study have not been published outside my thesis (Owen-Smith 1973). Thus I will use the white rhino as a special example, reporting aspects of its ecology in somewhat greater detail than is the case for other species, for which information has been extracted from the literature.

Other chapters analyze the relationships between particular features of the ecology of megaherbivores and body size. For these I draw on the now extensive body of facts published about the variety of ungulate species that still occur in Africa, and in some cases from data on ungulate species from other regions. In analyzing trends in aspects of ecology in relation to body mass for large herbivores, I will adopt a hypothetico-deductive approach. From a consideration of allometric relationships, a proposition will be made as to how a particular ecological attribute ought to vary with body mass. In general, hypotheses take the form that a certain proportional variation in body mass entails a corresponding proportional variation in an ecological feature. Such relationships imply power functions of the form $E = aM^b$, where E represents the ecological attribute, M body mass, a a constant, and b the power coefficient of the relation. These relations will be tested statistically by standard least-squares regression (Sokal & Rohlf 1969; Peters 1983). The confidence limits for the regression coefficient between log functions of E and M indicate whether or not the data refute the starting hypothesis. While the general trend with body mass indicates the constraining effect of increased body size on adaptations, points for individual species deviating markedly from the overall regression line suggest special adaptations releasing these species to some degree from the body size constraint. Special consideration will be given to the extent to which megaherbivores have compensated adaptively for the ecological restrictions imposed by their very large size.

The general questions underlying the body mass chapters are these:

1. To what extent do aspects of the ecology of megaherbivores differ in magnitude, and perhaps in kind, from those of smaller ungulates?
2. Do the ecological features shown by megaherbivores merely represent extrapolations of the trends with body size evident among large herbivores?
3. What features of ecology set upper limits to the body sizes attained by mammalian herbivores?
4. What are the special influences of megaherbivores on ecosystem processes?

Two chapters confront the two special problems posed by megaherbivores, from the perspective of the understanding gained from earlier chapters. Chapter 15 addresses the biological puzzle raised by the complete demise of megaherbivores outside Africa and tropical Asia during the late Pleistocene. I evaluate the relative role of climatic change and human overkill as causal factors in these extinctions, and advance a synthetic hypothesis taking into account features of the ecosystem impact of megaherbivores that have not been considered by other authors.

The effects of megaherbivores on ecosystem processes on the one hand, and their vulnerability to human disturbance on the other, create problems for their conservation. In chapter 16 I offer practical suggestions on how best to conserve and manage their populations within the limited confines of national parks and equivalent reserves, without negating the special features of the ecology of these large beasts. However their continued survival into the twenty-first century also raises political issues concerning how much space can be allocated to them alongside burgeoning human populations. To be successful these socio-political decisions must rest on a sound ecological knowledge of the sensitivities of these species, and also on an appreciation of the instrinsic value of conserving them.

In the final chapter I summarize the typifying ecological features of the megaherbivore phenotype. I hope that this book will help disseminate a more enlightened understanding of these great beasts, as an aid to effective action in ensuring their continued persistence on this planet; so that the final summary does not serve merely as an epitaph.

2

Morphology, evolutionary history and recent distribution

Introduction

Eight living species of terrestrial mammal fall into the megaherbivore category in terms of maximum body mass attained. These include two species of elephant, four rhinoceros species, and single species of hippopotamus and giraffe. In this chapter I describe the ecologically important features of their morphology, document their historic and present day geographic distributions, and outline their paleontological origins. This information serves as an essential background to the ecological topics that will form the subject of subsequent chapters.

Morphology

The most basic feature of significance to this book is size. How big do males and females of extant species of megaherbivore grow, in terms of height and weight? Size factors are frequently exaggerated in the literature, especially for large animals that are inconvenient to weigh. A distinction needs furthermore to be made between the asymptotic weights most typically reached by adult animals, and the maximum weights that might be reached by exceptional individuals. Weights may furthermore differ between different subspecies, and within populations in relation to prevailing resource abundance. Animals held in captivity may grow larger or smaller than their wild counterparts, depending on the adequacy of the diets that are provided to them.

Also of fundamental importance are the anatomic features functioning in the procurement and digestion of food. These include in particular the dentition and the structure of the digestive tract.

All large mammalian herbivores are dependent to some degree upon the agency of microbial symbionts for degradation of the cellulose in plant cell walls. To facilitate cell wall digestion, a gut compartment is needed where food passage can be delayed, and within which the conditions of neutral or slightly alkaline pH required by the bacteria and protozoa can be maintained. Mammalian herbivores fall into two categories in terms of the location of the fermentation chamber. Foregut fermenters have a compartment developed from the esophagus or anterior portion of the stomach. Distinct subdivisions may further compartmentalize this chamber, with narrow connecting openings delaying the passage of food material between them, as in ruminants such as bovines and deer. In such species absorption of fermentation products such as volatile fatty acids occurs before the food residues enter the acidic gastric chamber, where protein digestion is initiated. In hindgut fermenters (sometimes termed cecalids), fermentation occurs in the cecum, a blind sac branching from the junction of the small and large intestines, and/or in the large intestine or colon. Pockets and folds in the walls may retard passage of digesta through these hindgut chambers. Digestion and absorption of protein and soluble carbohydrates occurs before food residues undergo fermentation (Langer 1984).

Dental structure distinguishes browsers, feeding primarily on the leaves and stems of woody plants and dicotyledonous herbs, from grazers, eating primarily the leaves of grasses and sedges. Grazers exhibit finely textured surfaces on high-crowned molars for grinding the fine, fibrous and dusty leaves typical of graminoids. Browsers show lower-crowned molars with prominent cusps for dissecting the softer and thicker leaves and stems of dicotyledonous plants. Among ruminants there are further distinctions in the design of the digestive tract between grazers ('bulk and roughage feeders') and browsers (so-called 'concentrate selectors'). Grazers have a capacious fermentation chamber, narrow ostia and moderate surface papillation to cope with the slowly fermenting leaves of graminoids. Browsers have relatively smaller rumens with profuse papillae and larger connecting openings to process the faster digesting leaves of dicotyledonous plants (Hofmann 1973). Comparable differences probably exist among hindgut fermenters, but remain undocumented.

The African elephant (*Loxodonta africana*) is the largest living mammalian herbivore (Fig. 2.1). There are two subspecies: the bush elephant *L. a. africana*, and the forest elephant *L. a. cyclotis*. The forest subspecies is distinguished by downward pointing tusks, and appears to be slightly smaller in size than the bush elephant, though confirmatory weights are lacking (Kingdon 1979).

The largest recorded African elephant is an adult male shot in Angola. This animal measured 4.0 m high at the shoulder, and weighed an estimated 10 000 kg; but it was clearly exceptional. Elephants culled in Uganda and Zambia yielded an asymptotic shoulder height of 3.2 m, and masses of up to

Fig. 2.1 African elephant bull.

5500–6000 kg, among males. Females were somewhat smaller, weighing up to 2500–2800 kg on average, with a maximum of 3232 kg recorded. The asymptotic shoulder height was 2.7 m (maximum 2.9 m). Males show a growth surge between 20 and 30 years, so that full weight is attained relatively late in life. However, elephants in other parts of Africa may attain somewhat larger sizes. In the Gonarezhou Park in south-eastern Zimbabwe, female weights of up to 3800 kg were estimated from the hind leg mass. Zoo-kept females originating from Tanzania and Mozambique reached weights between 2800 kg and 3200 kg at 16 years, associated with shoulder heights of 2.5–2.9 m. A male of this group weighed 6600 kg and stood almost 3 m at the shoulder when destroyed at 25 years of age; while another captive male was still growing having reached a height of 3.25 m at 28 years. In the Kruger Park in South Africa, some exceptionally large bulls attained a shoulder height of 3.4 m (Bullock 1962; Hall-Martin 1987; Hanks 1972a; Lang 1980; Laws 1966; Sherry 1978).

The Asian or Indian elephant (*Elephas maximus*) (Fig. 2.2) is a little smaller than the African species. Captive females yielded shoulder heights of up to 2.35 m, while males measured up to 2.7 m. The mean weight

Fig. 2.2 Asian elephant (photo courtesy M. J. B. Green).

attained by females is reported to be 2720 kg, although a maximum weight of 4160 kg and shoulder height of 2.54 m is claimed. For males a maximum weight of 5400 kg, and shoulder height of 3.2 m, is reported; although the measured weight of one captive male was only 3600 kg (Hanks 1972a; Shoshani & Eisenberg 1982).

Elephants have the nasal region modified into a prehensile trunk serving as a food-gathering appendage. The upper incisor teeth have been transformed into enormous tusks. The molars replace one another in sequence, each tooth filling an arm of the short jaw so that no more than one and a half teeth are in operation on each half of the jaw. The teeth of Asian elephants are somewhat higher-crowned than those of the African elephant. In both species the enamel is folded into numerous plates, able to grind grasses as well as dicotyledonous browse. Female Asian elephants commonly lack tusks, but this pattern is relatively rare among African elephants. The stomach is simple, with the cecum not especially large relative to other parts of the gut, and the colon uncompartmentalized. Fermentation occurs both in the cecum and colon (Benedict 1936; Clemens & Maloiy 1982; Laws 1966; Maglio 1973).

The white or square-lipped rhinoceros (*Ceratotherium simum*) (Fig. 2.3) is generally regarded as third largest among living land mammals. However, there are no measured weights to confirm this. A young adult male (with the

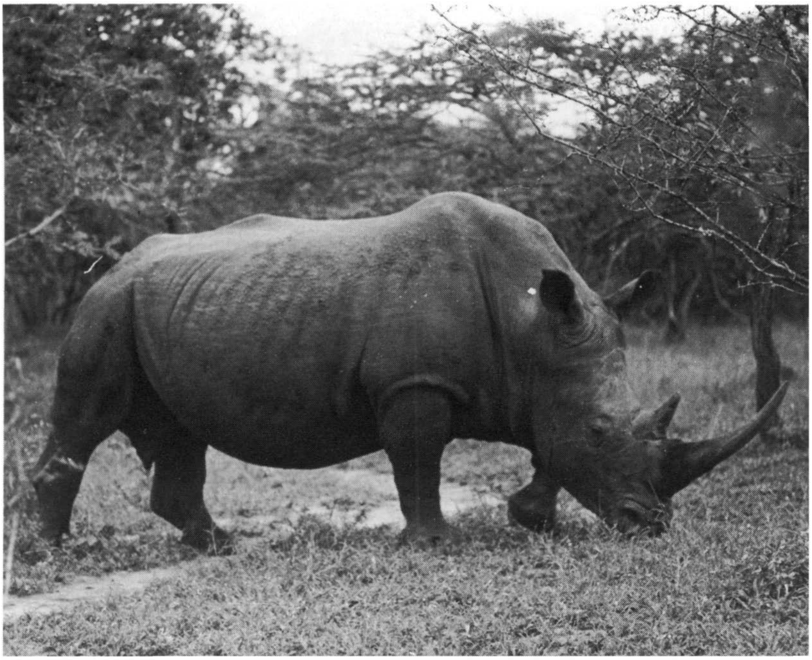


Fig. 2.3 White rhino bull.

last molar not fully erupted), destroyed and sectioned at Umfolozi for the purpose of estimating drug dosages required for immobilization, weighed 2130 kg (John Clark personal communication 1965). Field weights are estimated by Natal Parks Board personnel to be 2000–2300 kg for adult males, and about 1600 kg for adult females. A weight of about 1800 kg is reported for a zoo-kept female (Foose 1982). Males attain shoulder heights of up to 1.8 m, females up to 1.77 m (Heller 1913; Kirby 1920).

Two subspecies of white rhino are distinguished. Animals of the northern race (*C. s. cottoni*) are differentiated from those of the southern race (*C. s. simum*) by the flatter dorsal profile of their skulls, and by their somewhat smaller teeth. Northern animals appear somewhat higher-legged and less long in the body, and lack the body hair which is present, although very sparsely, on southern animals (Cave 1962; Heller 1913).

The African black or hook-lipped rhinoceros (*Diceros bicornis*) (Fig. 2.4) is somewhat smaller than the white rhino. East African specimens weigh up to 1313 kg, while in South Africa weights of 708–1022 kg for males and 718–1132 kg for females were measured. Shoulder heights vary between 1.4 m and 1.65 m (Meinertzhagen 1938; Hitchins 1968, and personal communication). Seven subspecies of black rhino have been described, but some of

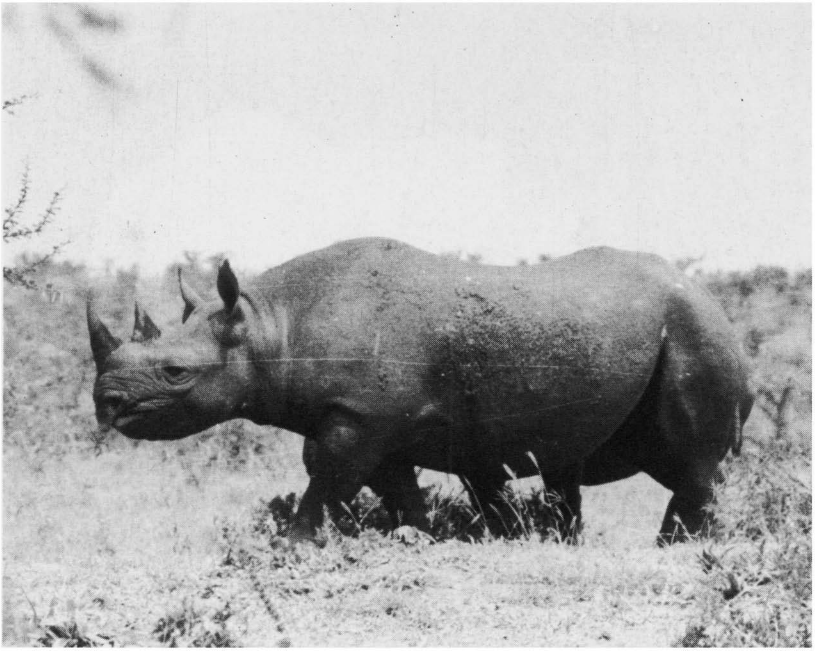


Fig. 2.4 Black rhino cow.

these are of uncertain status. The subspecies *D. b. bicornis* which inhabited the Cape was the largest. Although now extinct there, it has been suggested that animals surviving in northern Namibia may represent this form (Groves 1967; Hall-Martin 1985; Joubert 1970).

Both African rhino species lack incisors and canine teeth. The white rhino uses its broad lips to pluck grass, while in the black rhino the upper lip is modified into a finger-like projection which aids browsing. The white rhino has high-crowned molars and premolars, with fine surfaces adapted for grazing. In black rhinos the molars are lower-crowned with high cusps, in support of its browsing habits. White rhinos are further distinguished from black rhinos by their much longer heads, also an aid to grazing, and by the hump on the back of the neck formed by the hypertrophied nuchal ligament. Both species bear two horns on the snout. The horns of females tend to be longer and more slender than those of males. Some taxonomists regard the differences between the two species as trophic adaptations insufficient to warrant the generic distinction, and hence refer to the white rhino as *Diceros simus* (Cave 1962; Ellerman, Morrison-Scott & Hayman 1953).

There is no notable difference in skin color between the two species of

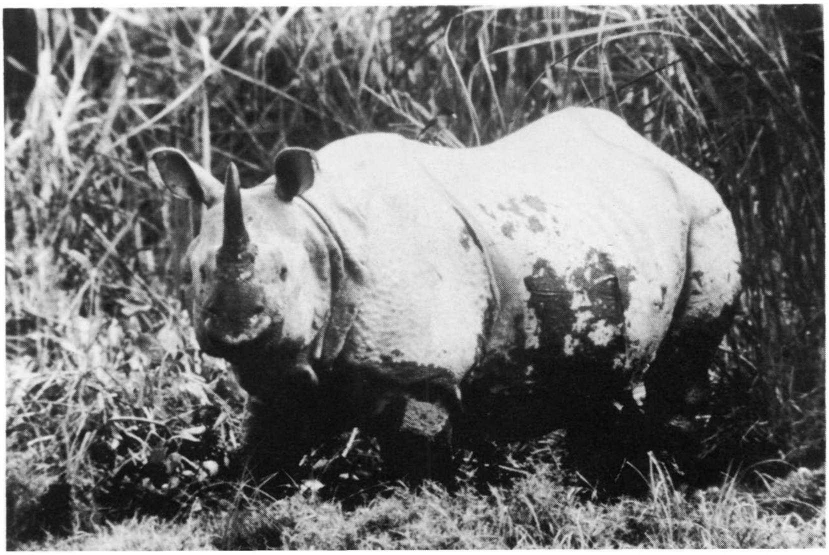


Fig. 2.5 Indian rhino (photo courtesy W. A. Laurie).

African rhino, this being influenced by the color of the soil last wallowed in. While it has been claimed that the appelation 'white' is a corruption of the Dutch word 'wijd', meaning wide, there is no basis for this conjecture. An early mention of the species in a document dated 1796–98 refers to the 'witte' (white) rhinoceros (du Plessis 1969); while Barrow (1801) mentions the supposed occurrence of a 'white rhinoceros' on the outskirts of the Cape settlement, distinguishing it by its 'pale carnation colour'. The most plausible explanation is that the first specimens to be encountered did in fact appear paler than the black rhinos inhabiting the fringe of the Cape settlement, probably as a result of wallowing in the calcareous soils typical of the northern Cape.

The Indian or great one-horned rhinoceros (*Rhinoceros unicornis*) (Fig. 2.5) is closely similar to the white rhino in size, although comparative measurements are sparse. Weights attained in the wild are estimated to be 2100 kg for males and 1600 kg for females; while a weight of about 1800 kg is reported for a captive female. Shoulder height may reach 1.8 m. The Javan or lesser one-horned rhinoceros (*Rhinoceros sondaicus*) is somewhat smaller, weighing up to about 1300 kg. Both of these species are characterized by a single horn on the snout, and by the retention of lower incisors, which have become modified into short tusks used in fighting. The prehensile upper lip of the Indian rhino aids feeding. The molars of the Indian rhino are

Fig. 2.6 Hippopotamus.

moderately high-crowned (although much less so than those of the white rhino), while the Javan rhino has molars that are relatively low-crowned and high-cusped, indicating a diet of browse (Foose 1982; Heller 1913; Laurie 1982; Thenius 1968).

The Sumatran or Asian two-horned rhinoceros (*Dicerorhinus sumatrensis*) attains a weight of about 800 kg and shoulder height of 1.2 m. It thus does not fall into the megaherbivore category, although I will report what is known about it for comparison with other rhinos. These animals are hairier than other living rhinos, and bear two fairly small horns on the snout. Incisors and canines are present in both jaws, while molars are low-crowned and high-cusped (Groves & Kurt 1972).

The digestive anatomy of rhinos resembles that of equids. In the black rhino the stomach is simple, the cecum voluminous and sacculated, and the colon also sacculated and compartmentalized. The chief site of fermentation is the cecum, with further fermentation occurring in the colon (Clemens & Maloiy 1982). Comparative descriptions are not available for other rhinos, although the basic pattern of the gut is similar.

For the hippopotamus (*Hippopotamus amphibius*) (Fig. 2.6) a maximum weight of 2660 kg has been reported for a male, which exceeds the weight attained by white rhinos; but this animal seems to have been exceptional.

The heaviest hippo shot during culling operations in Uganda was a female weighing 2025 kg, while in the Kruger Park in South Africa the heaviest animal culled was a male weighing 2005 kg. In Zambia the maximum recorded weight of animals culled in the Luangwa River was 1600 kg for males and 1565 kg for females. In the large sample of animals culled in Uganda the mean male weight was 1480 kg and the mean female weight 1365 kg. Hippos are semi-aquatic in habits, with a squat build and maximum shoulder height of about 1.4 m (Bere 1959; Marshall & Sayer 1976; Meinertzhagen 1938; Pienaar, van Wyk & Fairall 1966a).

Hippos retain incisor teeth, and have tusk-like canines used by males in fighting. The wide lips are used to pluck grass, and the molars are high-crowned. The stomach of a hippo is large and partly subdivided, creating some separation of contents between the anterior chambers and the posterior glandular section. Microbial fermentation occurs in the anterior sections. A cecum is lacking, and the large intestine is relatively undifferentiated. Despite forestomach fermentation, hippos do not remasticate food like ruminants (Clemens & Maloiy 1982; Langer 1976; van Hoven 1978).

Giraffe (*Giraffa camelopardalis*) (Fig. 2.7) attain maximum recorded weights of 1930 kg for a male and 1180 kg for a female. More typical weights are 1200 kg for adult males and 800 kg for adult females. Thus females generally do not reach the megaherbivore threshold as defined in this book. Giraffe are the tallest of living land mammals, with males reaching a maximum head height of 5.5 m, and females 4.5 m (Dagg & Foster 1976; Meinertzhagen 1938; Pellew 1984a).

Giraffe have a long, muscular tongue, which aids in gathering leaves into the mouth; and the dentition is typical of browsers. Giraffe are ruminants and like other ruminants chew the cud. The ruminoreticulum is relatively small, and the connecting ostia between compartments relatively large (Hofmann 1973).

The eight extant species of megaherbivore fall into four clusters in terms of body size: (i) the two elephants, with adult female weights of 2500–3800 kg; (ii) white rhino, Indian rhino and hippo, with adult female weights of 1400–2000 kg; (iii) black rhino and Javan rhino, with adult females weighing 1000–1300 kg; (iv) giraffe, with adult female weights of 800–1200 kg. The next largest mammalian herbivore is the Asian gaur, with adult males weighing as much as 940 kg. American bison bulls weigh up to about 900 kg, while African buffalo weigh up to 860 kg. Record specimens of these species could possibly reach 1000 kg, but such weights are exceptional. (See Appendix I for scientific names and maximum and mean weights for all large herbivores referred to in the book).

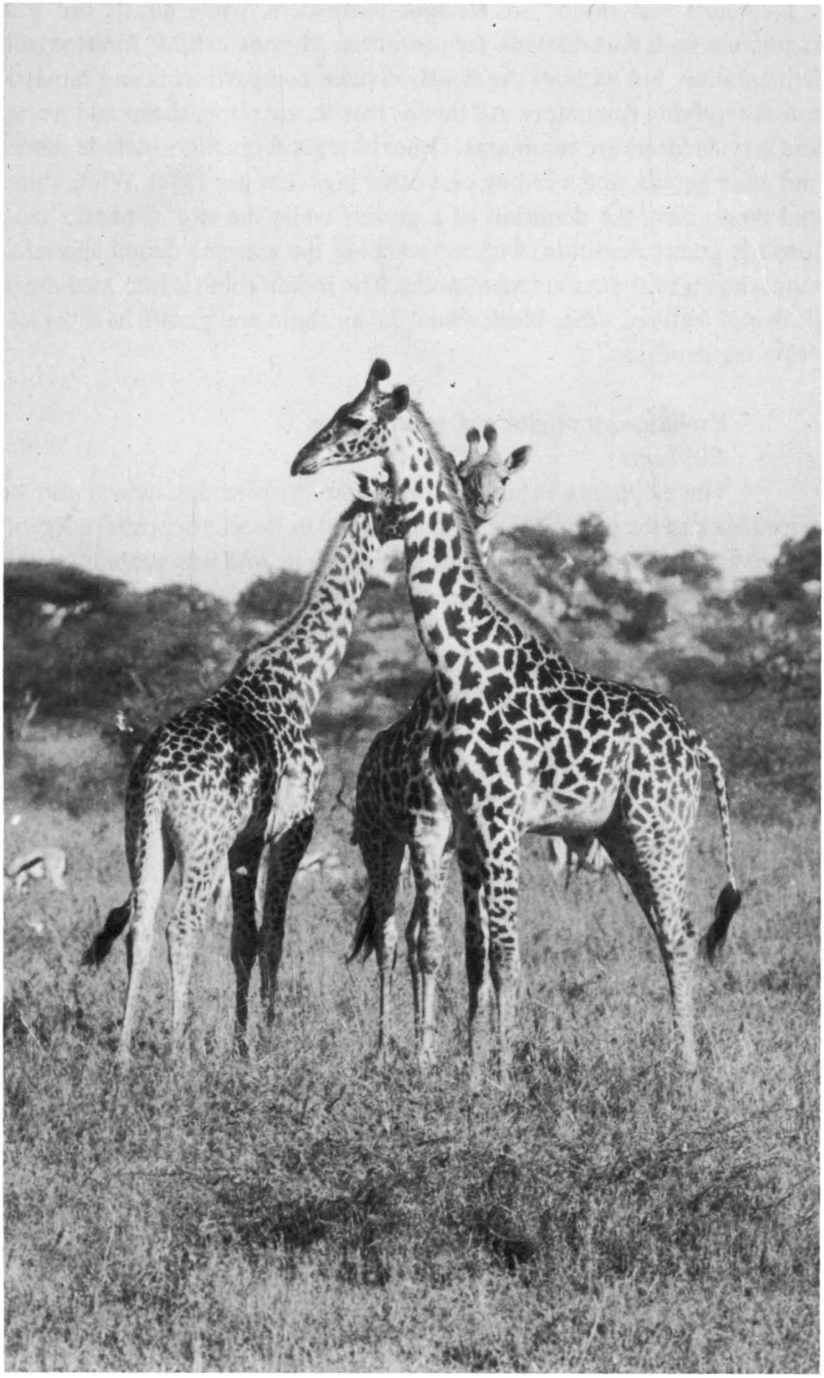


Fig. 2.7 Giraffe.

Elephants and rhinos are hindgut fermenters, while giraffe are true ruminants with forestomach fermentation. Hippos exhibit forestomach fermentation, but without the clearly divided compartments and remastication typifying ruminants. All bovids (cattle, antelope, sheep and goats) and cervids (deer) are ruminants. Other hindgut fermenters include zebras and other equids, and warthog plus other pigs (Langer 1984). White rhino and hippo have the dentition of a grazer; while the two elephants tend towards grazer dentition, without reaching the extreme dental specialization shown by the extinct mammoths. The Indian rhino is intermediate in its dental features, while black rhino, Javan rhino and giraffe have typical browsing dentition.

Evolutionary origins and relationships

Elephants

The elephants belong to the order Proboscidea, which can be traced back to the genus *Moeritherium*, found in Eocene deposits in Egypt. *Moeritherium* had the form of a stout-legged pig, and was probably semi-aquatic in its habits. Its descendants showed early tendencies towards elongation of the upper lip and nose, development of incisor teeth into tusks, and greatly increased body size. The deinotheres, which appeared in Africa during the Miocene and persisted in Eurasia through the Pliocene, had lower incisors which curved downwards and backwards in the form of huge hooks. In gomphotheres of this time the lower jaw was greatly lengthened, with tusks present in both upper and lower jaws (Maglio 1973; Coppens *et al.* 1978).

The modern day elephants are descended from gomphothere ancestors. The earliest recognized elephant, *Primelephas*, made its appearance in Africa during the late Miocene. It was ancestral to both of the extant genera, *Loxodonta* and *Elephas*, as well as to the mammoths (*Mammuthus*).

Loxodonta is the most conservative of these genera in its dental features, although early forms showed changes in the center of gravity of the jaw and height of the skull which developed somewhat later in other elephant lineages. It has remained exclusively African in its distribution. *Loxodonta atlantica*, which persisted until the mid Pleistocene, was larger than the modern African elephant, and also somewhat more progressive in its dentition. The living species, *L. africana*, first appeared during the late Pliocene, but from the paucity of fossil remains appears at that time to have been restricted to forest habitats. It does not become prominent in deposits at Olduvai Gorge in Tanzania and other savanna regions until late in the Pleistocene.

The genus *Elephas* appeared in both Africa and Eurasia during the mid Pleistocene. The African species *E. recki* exhibited molars which were higher crowned and more complexly folded than those of *L. atlantica*. *E. recki* and its descendant *E. iolensis*, similarly adapted for grazing, remained the most common elephant species in East African fossil deposits until about 35 000 years BP, when the lineage went extinct. The genus died out in Europe at about the same time, but in Asia it has persisted to the present day in the form of the Asian elephant *E. maximus*.

The genus *Mammuthus* originated in Africa during the mid Pliocene, but had disappeared from this continent by the early Pleistocene. Its main center of radiation was Eurasia, and mammoths entered North America fairly late in the Pleistocene. *Mammuthus* was the most advanced genus among the elephants in terms of its dental and cranial features – most particularly in its very high-crowned molars with their extremely complex pattern of fine enamel ridges, clearly specialized for grazing fibrous and abrasive forage. Other notable adaptations are the paired finger-like extensions on the tip of the trunk, combined with lateral wing-like extensions, which could have aided the gathering of grass (Guthrie 1982). With a shoulder height of over 4.0 m, the mid Pleistocene species *M. armenicus* was the largest of all proboscideans. The woolly mammoth *M. primigenius*, which persisted in both Europe and North America until the end of the last glacial, was somewhat smaller, with a shoulder height of about 2.8 m (Fig. 2.8).

Allied with the true elephants are the mastodonts of the family Mammutidae. Their prime distinguishing feature is the prominent mammary-gland-like cusps on their molar teeth, an indication of a primarily browsing diet. Mastodonts became extinct in Europe during the early Pleistocene, but persisted in North America until the end of the Pleistocene. Three genera of gomphotheres were also represented in South America during the Pleistocene. Among these *Stegomastodon* showed dental adaptations for grazing (E. Anderson 1984).

Rhinoceroses

A possible precursor of the Rhinocerotidae (order Perissodactyla) is the genus *Hyrachyus*, found in late Eocene deposits in North America and Asia. These were small, light-bodied animals, hardly different from the first horses and tapirs. Descendants soon exhibited a tendency towards large body size and towards the development of peculiar boneless horns, the presence of which is revealed by roughened areas on the fossilized skulls.

Baluchitherium, a rhinocerotid which occurred in Asia during the

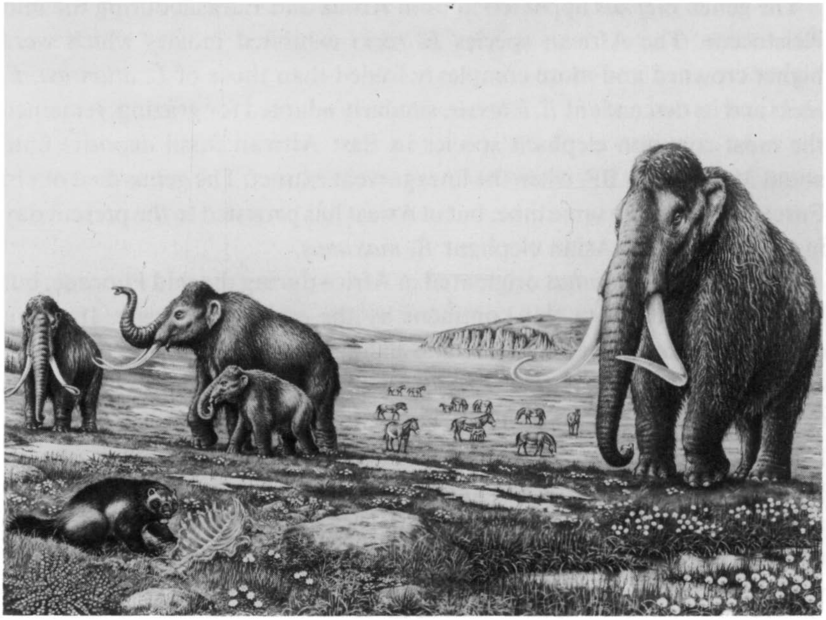


Fig. 2.8 Mammoth (photo courtesy British Museum (Natural History)).

Oligocene and early Miocene, was the largest land mammal ever to walk the earth. It had a shoulder height of over 5 m, and was massively built. *Teleoceros*, a squat, heavy-bodied rhinoceros that lived in North America during the Miocene and early Pliocene, had a single small horn on the end of its snout; while the Miocene diceratheres exhibited two small nasal horns arranged side by side. *Elasmotherium*, from the Pleistocene steppes of Eurasia, had a gigantic single horn on its forehead. Rhinoceroses exhibited their greatest abundance during the latter half of the Tertiary era, and their generic richness had declined by the beginning of the Pleistocene (Colbert 1969).

The five living species of rhinoceros fall into three distinct subfamilies, which have had independent evolutionary histories for some time. The Asian one-horned rhinos belong to the subfamily Rhinocerotinae, which can be traced back to the Miocene genus *Gaindatherium*, found in the Sivalik hills of northern India. This subfamily is characterized by the single nasal horn, and by the retention of lower incisors, which have become modified into short tusks used in fighting. Of the two surviving species the Javan rhino is the more primitive, having altered little since the late Miocene some ten million years ago (Thenius 1969).

The Asian two-horned rhinos or Dicerorhinae can be traced back some forty million years to the tapir-sized *Dicerorhinus tagicus* from the Oligocene. The extant Sumatran rhino differs relatively little from its Oligocene predecessors. Four other species of this subfamily occurred in Europe during the course of the Pleistocene, including Merck's rhinoceros (*Dicerorhinus kirchbergensis*) as well as the woolly rhino (*Coelodonta antiquitatis*). The woolly rhino paralleled the white rhino in its high-crowned molars, absence of incisor and canine teeth, lengthened skull and other adaptations indicating a mainly graminoid diet. However it was somewhat smaller, attaining an estimated body mass of about 1100 kg. The giant *Elasmotherium* (of uncertain affinities) had enormous evergrowing molars with a complex enamel pattern, and was clearly also a grass-feeder (Fortelius 1982, and personal communication).

The African rhinos, or Dicerinae, are distinguished from the Dicerorhinae primarily by their lack of any ossification of the nasal septum. Both modern species lack incisor as well as canine teeth. The finding of the aberrant genus *Paradiceros* in Miocene deposits in Kenya suggests that the group had an independent African origin. The earliest known *Diceros* species, *D. pachygnathus* and *D. dourariensis*, occurred in North Africa and adjacent parts of the Mediterranean region during the late Miocene. The modern black rhinoceros *D. bicornis* made its earliest appearance in Pliocene deposits dated at four million years BP, and by 2.5 million years BP its teeth had become indistinguishable from those of the modern representatives. The white rhinoceros lineage first appears in the form of the species *Ceratotherium praecox* in Pliocene deposits in Kenya dated at about seven million years BP. This ancestral form retained four incisors in the upper jaw, while its molars were not as high-crowned as those of the modern species. It was also somewhat larger than living white rhinos. *C. praecox* is abundant in fossil deposits at Langebaanweg in the Cape dated at 4–5 million years ago, so that its range was continent-wide. The modern species *C. simum* appears 3–4 million years ago in fossil deposits in East Africa, and is especially abundant in the Pleistocene deposits at Olduvai Gorge. The fossil evidence thus suggests a splitting of *Ceratotherium* from *Diceros* during the course of the early Pliocene (Hooijer 1969; Hooijer & Patterson 1972).

Hippopotamuses

The ancestors to the Hippopotamidae (order Artiodactyla) were the Anthracotheriidae, a widespread family of large, pig-like animals which occurred from the Oligocene to the late Pliocene. Genera such as *Merycopotamus* resembled modern hippos to a remarkable degree. True hippos appeared in Africa during the Pliocene, spreading later to southern Europe and Asia. The species *Hippopotamus antiquus* was especially common in Europe, including the British Isles, during Pleistocene interglacials. In Africa two species coexisted during the Pleistocene. The extinct *H. gorgops* had a longer and shallower skull, more elevated orbits and larger mandible than the modern hippo *H. amphibius*. The living pigmy hippo *Hexaprotodon liberiensis* is a tapir-sized animal, but extinct forms of *Hexaprotodon* attained sizes approaching those of living hippopotamus (Coryndon 1978).

Giraffes

Included among Giraffidae (order Artiodactyla) was the extinct genus *Sivatherium*, which occurred in both Africa and Eurasia during the Pliocene and early Pleistocene. Representatives attained shoulder heights of over 2.0 m, and with their massive build may have come marginally into the megaherbivore range. The earliest representatives of *Giraffa* appeared in Africa during the late Miocene. Giraffes occurred in southern Eurasia as well as in Africa during the Pliocene and Pleistocene (Churcher 1978).

Summary

Extant megaherbivores thus represent four mammalian families falling into three distinct orders. African and Asian rhinos are rather distantly related to each other, while the two elephant species are somewhat more closely allied. These species cannot be regarded as especially primitive in their evolutionary origins, except perhaps for the Javan rhino. All surviving species, except for the Javan rhino, date from the Pliocene radiations when most of the extant species of bovid and cervid also originated.

Paleontological diversity

Very large mammals were prominent in world faunas throughout the Tertiary and into the Quaternary. Apart from the proboscideans and rhinocerotids mentioned above, similar body sizes were attained by other forms of mammal. In the Americas giant ground sloths of the genera *Megatherium* and *Eremotherium* reached estimated masses of 3500 kg, while certain of the grazing mylodonts probably weighed over 1500 kg. The notoungulate genus *Toxodon* attained hippo-like proportions in South America; while the Australian marsupial *Diprotodon* was rhino-like in its build. The extinct South American camelid *Titanocamelops* reached a head height of 3.5 m, and was the local counterpart of the giraffe. Extinct forms of *Bison* such as *B. antiquus* and *B. latifrons* may have exceeded 1000 kg in maximum weight, but such sizes were probably attained only by the largest males. No bovid falls truly into the megaherbivore category.

During the course of the Pliocene and Pleistocene, megaherbivores were represented among fourteen mammalian families: the Diprotodontidae among the Marsupiala; the Megatheriidae and Mylodontidae in the Edentata; the Toxodontidae in the Notoungulata; the Gomphotheriidae, Deinotheriidae, Stegodontidae, Mammutidae and Elephantidae of the order Proboscidea; the Rhinocerotidae and Chalicotheriidae of the Perissodactyla; and the Anthracotheriidae, Hippopotamidae and Giraffidae among the Artiodactyla (Table 2.1). Throughout the course of the Pleistocene these families were represented by over 20 genera, and a somewhat greater number of species, worldwide (Table 2.2). Within regional faunas there were commonly between two and six species of megaherbivore, including perhaps two proboscideans, one or two rhinoceroses, a hippo-like animal, and perhaps a giant ground sloth or tall giraffe-like browser. Megaherbivores occurred in a complete range of ecosystems, from tropical forest and savanna, through deciduous and coniferous woodland, to the open grassy steppe of the subarctic during the ice ages.

The generic diversity of megaherbivores declined only slightly over the five million years of the Pliocene and Pleistocene. This was due mainly to a reduction in the number of proboscidean genera (Table 2.2). Between the late Pleistocene and the Holocene there was a dramatic reduction in diversity affecting all orders. Only three out of six orders persisted into the Holocene. While megaherbivores were formerly represented worldwide, surviving forms are restricted to the Old World tropics and subtropics of Africa and Asia.

Distribution of extant species

All surviving species of megaherbivore have become somewhat restricted in numbers and range in modern times compared with their early historic distribution.

Historically the African elephant was distributed continent-wide, from the environs of Cape Town to the fringe of the Sahara. In Roman times it evidently occurred also in the Mediterranean region. It is still represented today through much of this region, although its distribution has become somewhat fragmented. The species occupies habitats ranging from equatorial rain forest through various forms of savanna to semidesert in Namibia and Mali. Its center of greatest abundance seems to be the broad savanna woodland region extending through central and eastern Africa;

Table 2.1. *List of the genera of megaherbivores extant during Pliocene, Pleistocene and Recent times*

Taxon	Time period	Geographic range
Marsupiala		
Diprotodontidae		
Diprotodon	Pleistocene	Australia
Edentata		
Megatheriidae		
Megatherium	Pleistocene	South America
Eremotherium	Pleistocene	South and North America
Mylodontidae		
Mylodon	Pleistocene	South America
Notoungulata		
Toxodontidae		
Toxodon	Pleistocene	South America
Proboscidea		
Gomphotheriidae		
Anancus	Miocene–M. Pleistocene	Africa, Eurasia
Cuvieronius	Pliocene–L. Pleistocene	South and North America
Haplomastodon	L. Pleistocene	South America
Stegomastodon	Pliocene–L. Pleistocene	South and North America
Deinotheriidae		
Amebelodon	Miocene–E. Pliocene	Europe, North America
Deinotherium	Miocene–E. Pleistocene	Africa, Asia, Europe
Gnathobelodon	Pliocene	Europe
Platybelodon	Miocene–E. Pliocene	Asia
Stegodontidae		
Stegodon	L. Pliocene–L. Pleistocene	Africa, Asia
Stegolophodon	L. Pliocene	Eurasia
Mammutidae		
Mammut	E. Miocene–L. Pleistocene	Eurasia, North America
Zygolophodon	Pliocene	Africa, Europe
Elephantidae		
Elephas	E. Pliocene–Recent	Africa, Asia, Europe
Loxodonta	M. Pliocene–Recent	Africa
Mammuthus	E. Pliocene–L. Pleistocene	Africa, Eurasia, North America
Primelephas	Miocene–E. Pliocene	Africa
Stegodibelodon	Miocene–E. Pliocene	Africa
Perissodactyla		
Rhinocerotidae		
Ceratotherium	M. Pliocene–Recent	Africa
Coelodonta	E.–L. Pleistocene	Eurasia
Dicerorhinus	Oligocene–Recent	Europe and Asia

Table 2.1. (*cont.*)

Taxon	Time period	Geographic range
Diceros	E. Pliocene–Recent	Africa, S. Europe
Elasmotherium	M.–L. Pleistocene	Asia
Rhinoceros	E. Pliocene–Recent	Asia
Sinotherium	Pliocene	Asia
Teleoceras	Miocene–E. Pliocene	Eurasia, North America
Chalicotheriidae		
Ancyclotherium	Pliocene–E. Pleistocene	Africa, S. Eurasia
Artiodactyla		
Anthracotheriidae		
Merycopotamus	Miocene–L. Pliocene	Africa, Asia
Hippopotamidae		
Hexaprotodon	Pliocene–Recent	Africa, Asia
Hippopotamus	Miocene–Recent	Africa, Eurasia
Giraffidae		
Giraffa	Miocene–Recent	Africa, Eurasia
Sivatherium	E. Pliocene–M. Pleistocene	Africa, Asia

Sources: Compiled from Martin and Guilday (1967), Kurtén (1968), Maglio & Cooke (1978), Kurtén and Anderson (1980), Simpson (1980), E. Anderson (1984) and Martin (1984a).

Note: E. Pleistocene = early Pleistocene
M. Pleistocene = middle Pleistocene
L. Pleistocene = late Pleistocene

although large numbers also occur in the forests of Zaire and Gabon, judging from the amount of ivory of the forest race coming onto the market. The current world population of African elephants totals under one million, and numbers are diminishing rapidly (Cumming & Jackson 1984; Douglas-Hamilton 1987; Kingdon 1982).

The Asian elephant was formerly distributed through most of tropical Asia, from India and Sri Lanka through to Malaysia, Indonesia and southern China. Today remnant populations persist in the wild in parts of Sri Lanka, south-eastern India, Assam, Burma, Thailand, Malaya and most of the larger islands of the Malaysian and Indonesian archipelago. The species occupies both forest and open woodland habitats (Eltringham 1982).

The hippopotamus was distributed in historic times from the Cape to the upper Nile River, wherever suitable water bodies occurred. The species still occurs today over much of this range, with its center of greatest abundance in the lakes of the western rift valley along the Uganda–Zaire border. In the

Table 2.2. *Numbers of megaherbivore genera represented in various continental faunas during different time periods*

Continent	Time period	Order Marsupiala	Edentata	Notoungulata	Proboscidea	Perissodactyla	Artiodactyla	Total
Africa	Pliocene	0	0	0	8	3	4	15
	Early Pleistocene	0	0	0	5	3	4	12
	Mid Pleistocene	0	0	0	3	2	4	9
	Late Pleistocene	0	0	0	2	2	2	6
	Recent	0	0	0	1	2	2	5
Asia	Pliocene	0	0	0	6	3	4	13
	Early Pleistocene	0	0	0	5	3	3	11
	Mid Pleistocene	0	0	0	3	4	2	9
	Late Pleistocene	0	0	0	2	4	1	7
	Recent	0	0	0	1	2	0	3
Europe	Pliocene	0	0	0	7	3	2	12
	Early Pleistocene	0	0	0	4	2	1	7
	Mid Pleistocene	0	0	0	2	2	1	5
	Late Pleistocene	0	0	0	2	2	1	5
	Recent	0	0	0	0	0	0	0
North America	Pliocene	0	0	0	3	1	0	4
	Early Pleistocene	0	1	0	4	0	0	5
	Mid Pleistocene	0	1	0	3	0	0	4
	Late Pleistocene	0	1	0	3	0	0	4
	Recent	0	0	0	0	0	0	0
South America	Pliocene	0	0	1	0	0	0	1
	Early Pleistocene	0	2	1	2	0	0	5
	Mid Pleistocene	0	2	1	2	0	0	5
	Late Pleistocene	0	3	1	3	0	0	7
	Recent	0	0	0	0	0	0	0
Australia	Pliocene	1	0	0	0	0	0	1
	Early Pleistocene	1	0	0	0	0	0	1
	Mid Pleistocene	1	0	0	0	0	0	1
	Late Pleistocene	1	0	0	0	0	0	1
	Recent	0	0	0	0	0	0	0
World	Pliocene	1	0	1	15	7	4	28
	Early Pleistocene	1	3	1	9	6	4	24
	Mid Pleistocene	1	3	1	8	6	4	23
	Late Pleistocene	1	3	1	8	6	2	21
	Recent	0	0	0	2	4	2	8

Sources: Compiled from Kurtén (1968), Maglio (1978), Kurtén and Anderson (1980), Simpson (1980), E. Anderson (1984), and Martin (1984a).

Pleistocene its range extended quite far northwards in Europe during interglacial periods (Kingdon 1979).

Giraffe remain widely distributed through savanna regions, from the Kalahari and Transvaal lowveld in the south to Mali and Somalia in the north. The historic range did not extend south of the Pongola River into Natal, but animals have been introduced into wildlife reserves in Zululand and are thriving there. In central Africa the species shows a distribution gap associated with the miombo woodlands of Zambia and southern Tanzania, apart from an isolated population in the Luangwa valley (Kingdon 1982).

The distribution of the Indian rhino was limited historically to north India and adjacent regions of Nepal. The habitats that it occupies consist of tall floodplain grassland and adjacent woodland. Today it occurs only in a few reserves in Assam and Nepal, the total population numbering about 1700 animals (Laurie 1982).

The Javan rhino was formerly widely distributed through most of south-east Asia from India to China and southwards through Indonesia. It generally occupied lowland forest. The current population is 55 animals restricted to the western tip of Java (Schenkel & Schenkel-Hulliger 1969b; Hoogerwerf 1970). The Sumatran rhino formerly ranged from Assam through to Vietnam and the islands of Borneo and Sumatra. It seems to favor more broken mountainous forest than the Javan rhino. About 700–800 animals remain, thinly scattered through Sumatra, Malaya, Borneo, Thailand and Burma (Borner 1979).

The historic distribution of the black rhinoceros was almost as wide as that of the African elephant, extending from the south-western Cape to Somaliland and the northern Cameroons–Ivory Coast border. However, the species was absent from the equatorial forest region of central Africa, its favored habitats being drier savanna and arid shrub steppe. Today, black rhinos survive in scattered population fragments through this range. The large populations that formerly occurred in the Luangwa Valley in Zambia and in southern Tanzania have been reduced to small remnants by poaching, and the largest surviving population is currently that in the Zambezi valley. Latest (1986) estimates indicate that only about 4500 black rhinos remain in Africa (Kingdon 1979; unpublished reports of the African Rhino and Elephant Specialist Group of the IUCN).

The white rhinoceros was distributed historically in the form of two discrete populations, separated by a gap of over 2000 km (Fig. 2.9). The species did not occur south of the Orange River in historic times, while in the east its southern limit was the region of the present-day Umfolozi Game Reserve. The northern boundary of the range of the southern race was the

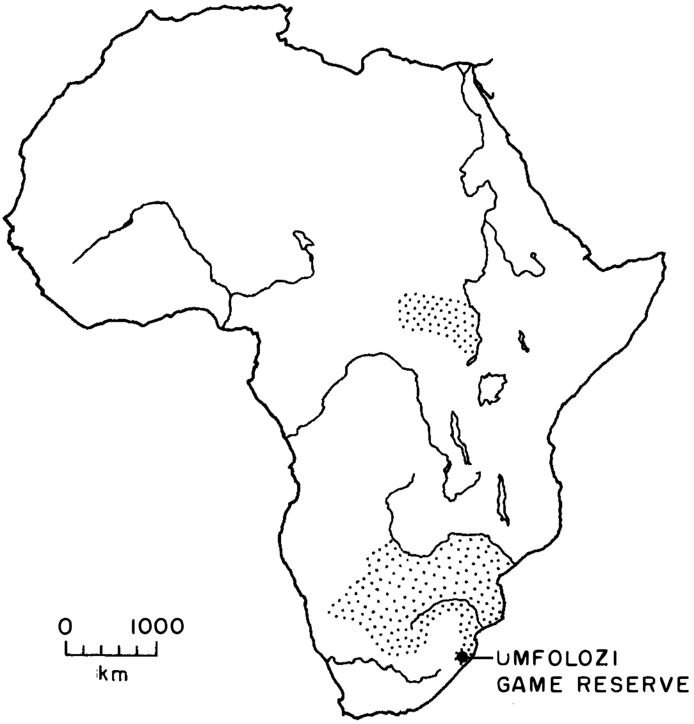


Fig. 2.9 Historic distribution of the white rhino. Distributional limits of southern population adapted from Huntley (1967). Distributional limits of northern population from Lang (1920).

Zambezi River and the region of the Namibia–Angola border (Huntley 1967). White rhinos were particularly abundant in eastern Botswana and adjacent parts of the western Transvaal. For example Harris (1838) reported seeing 80 in a day's march north of the Magaliesberg Range towards the upper Limpopo River. Favored habitats seem to have been semi-arid savanna, although in Zimbabwe animals were commonly associated with drainage line grasslands (Kirby 1920; Selous 1899).

The northern subspecies was found only to the west of the Nile River, from northern Uganda northwards to the vicinity of Shambe in the Sudan, and westwards into the Central African Republic. This northern range is associated mostly with mesic, *Combretum*-dominated savanna with tall grass prevalent except after fires. Although there are no historic records of white rhinos in East Africa, teeth found in Kenya and Tanzania suggest that the species occurred there during the Holocene. Rock engravings in Algeria indicate that the species was present in North Africa perhaps 5000–10 000 years ago (Heller 1913; Hooijer & Patterson 1972; Lang 1920, 1923).

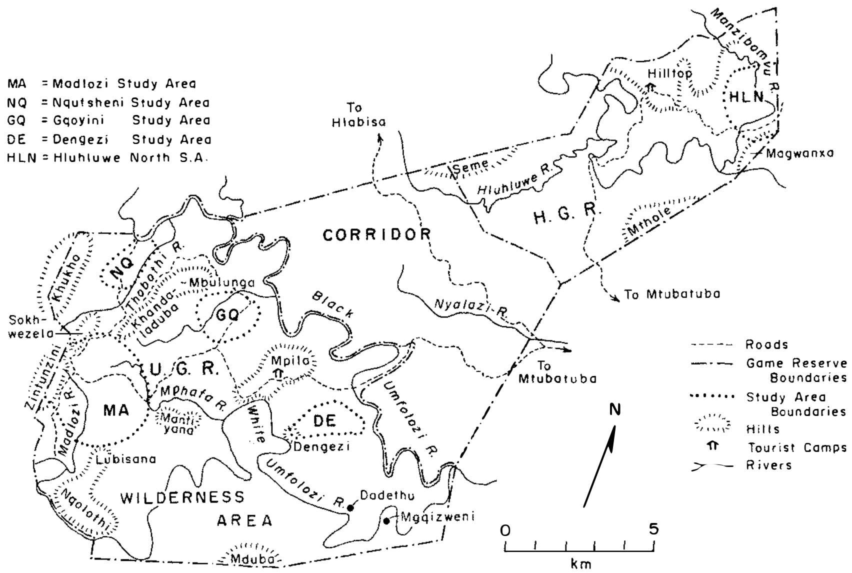


Fig. 2.10 The Umfolozi–Corridor–Hluhluwe Game Reserve complex, showing locations of main features and of the intensive study areas.

The northern race of white rhino numbered about 2000 animals during the early 1960s. In 1980 an estimated 800 white rhinos still survived in Sudan and north-eastern Zaire; but the population has since been decimated by poaching for the horns, so that at the time of writing only 17 animals remain, all in the Garamba Park in Zaire (Schomber 1966; Hillman-Smith, Oyisenzoo & Smith 1986).

White rhinos were exterminated in southern Africa during the late nineteenth century, except for a few score surviving at the southern limit of the range between the Black and the White Umfolozi rivers in Zululand (although another remnant survived in the Nuanetsi region of Mozambique until the 1930s). The Umfolozi Game Reserve was proclaimed in 1898 to protect the last survivors, although protection did not become effective until 1920 (Sidney 1966; Vincent 1970).

Since then numbers have increased steadily to reach a peak of 2000 animals in the Umfolozi–Hluhluwe region in 1970. Starting in the 1960s, animals have been translocated from this population to restock other areas where the species formerly occurred. The current total population numbers about 4000 white rhinos, over half of which now occur outside the Umfolozi–Hluhluwe Reserve.

My study of the white rhino was carried out in the Umfolozi Game Reserve and neighboring Hluhluwe Reserve in Zululand (Fig. 2.10).

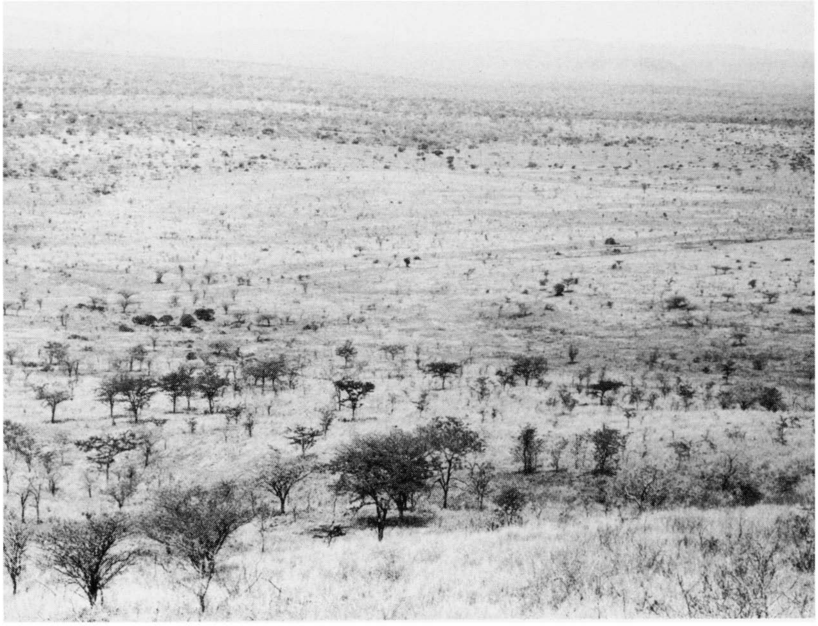


Fig. 2.11 View over the white rhino study area in the western region of Umfolozi Game Reserve.

Following an initial survey in 1966, the main study period extended from November 1968 to September 1971. Most intensive observations were carried out near the Madlozi outpost in the western region of the Umfolozi Reserve, where the highest densities of white rhinos existed (Fig. 2.11).

The Umfolozi Game Reserve covers an area of about 450 km², and is joined to the Hluhluwe Reserve by an intervening area of State Land known as the Corridor. The total extent of this unit, termed the Umfolozi–Hluhluwe complex, is about 950 km². The Umfolozi section consists of mostly gently rolling thorn savanna, underlaid by relatively fertile soils derived from Ecca shales and sandstones of the Karroo formation. In the Hluhluwe Reserve the country is more steeply rolling with open grassy hills and forest patches. The climate in Umfolozi is hot, with mean daily maximum temperatures of 32.6 °C in January (mid-summer) and 25.3 °C in July (mid-winter). The corresponding mean daily minima are 21.8 °C and 13.2 °C. The mean annual rainfall at Mpila Camp in Umfolozi is 700 mm (1959–1980), 70% of which falls during the six summer months of October to March. Rainfall increases northwards to reach a mean of 985 mm (1932–1980) at Hilltop Camp in Hluhluwe. The vegetation in Umfolozi is dominated by small trees and shrubs of the genus *Acacia* in the woody layer, and the grass *Themeda triandra* in the herb layer, although extensive areas of mixed short grasses occur.

In summary, most of the extant species of megaherbivore had a nearly continent-wide distribution in early historic times, wherever suitable savanna or forest environments occurred. The exceptions are the Indian rhino and, to a lesser degree, the white rhino. However, the white rhino was widely distributed through Africa during the Pleistocene, and there is evidence that its disappearance from East Africa was relatively recent. Other ungulate species with comparably wide historic distributions in Africa include warthog, bushpig, bushbuck and African buffalo; while those widely distributed through tropical Asia include water buffalo, sambar deer and muntjac.

All three Asian species of megaherbivore have become greatly restricted in geographic range, with the Javan rhino poised on the verge of extinction. The white rhino was hunted to near extinction in southern Africa during the last century, but has since recovered under protection. However the northern race of white rhino has been reduced to critically low numbers in the past few years. Black rhinos numbers are dwindling rapidly. While the current status of the African elephant is healthy overall, populations are undergoing steady attrition.

3

Food and other habitat resources

Introduction

The habitat resources of interest to this chapter are those that individual animals of a species depend upon for their survival. These include food sources, surface water, and refuges from weather extremes.

Food

For large herbivores dietary intake may be characterized either in terms of (i) the plant species eaten, (ii) the plant parts ingested, or (iii) the nutrient contents of the ingested material.

In terms of plant species, the basic classification is in terms of the graminoid:dicotyledon proportions (including non-graminaceous monocots with dicots). The leaves of grasses have higher contents of fibrous cell wall components, and digest more slowly, than the leaves of woody and herbaceous dicots. Silica bodies present in grass leaves further reduce digestibility and also abrade teeth. However, the leaves of woody dicots are ultimately less digestible than those of grasses, due to a higher proportion of indigestible lignin incorporated in the cell wall. Furthermore, the leaves of woody and herbaceous dicots frequently contain toxic or digestibility-reducing compounds, which are much less common in grasses.

In terms of plant parts, the proportions of foliage, stemmy material and fruits in the diet are of interest. Supporting tissues such as stems and bark tend to be high in indigestible fiber, while fruit pulp and seeds contain stores of soluble carbohydrates. Leaves contain the photosynthetic enzymes and are highest in protein and minerals (apart from calcium), although protein content declines as leaves age and fiber contents increase.

Nutrient content is most widely expressed in terms of the 'crude protein' (nitrogen × 6.25) concentration in the dry matter. Energy availability is dependent upon the digestibility of the structural carbohydrates (cellulose and hemicellulose) forming, together with lignin, the cell walls. However, the overall dry matter digestibility tends to be closely related to the crude protein content (Owen-Smith 1982).

In most environments food abundance and quality change seasonally due to the phenology of plant growth. Food quality is highest early in the growing season due to the prevalence of new leaves and shoots, while food abundance peaks later in the growing season. During the dormant season many woody plants shed their leaves, while grasses withdraw nutrients and leave standing dead leaves. However fruits and seeds may provide a high quality supplement during the early part of the dormant period.

Nutritional balance depends most directly not on the potential food abundance in the vegetation, but on the rate of food ingestion and on the nutritional value of the ingested material. Defecation rates provide an indication of food passage rates, and, indirectly, of daily food intake (allowing for digestibility).

Diet composition

Elephants

African elephants exhibit much variation in grass:browse proportions in the diet (Table 3.1). Under open grassland conditions, such as prevail in the Murchison Falls and Queen Elizabeth National Parks in Uganda, grass may form 60–95% of the diet year-round. In wooded savannas in Kenya, Uganda, Zambia, Zimbabwe and Tanzania, grass occupies between 40% and 70% of the feeding time during the wet season, but only 2% to 40% during dry season months. Bulls tend to select slightly higher proportions of grass than cows. Grass is insignificant in the diet of elephants inhabiting forests in Ghana and Ivory Coast, where woody browse and fruits are the main food components. Fruits and seed pods are also actively sought out by savanna elephants when available (Barnes 1982a; Buss 1961; Field 1971; Field & Ross 1976; Guy 1976a; Laws & Parker 1968; Lewis 1986; Merz 1981; Napier Bax & Sheldrick 1963; Short 1981; Williamson 1975a).

When feeding on grasses, African elephants favor leaves and inflorescences during the wet season. Commonly eaten species include short grasses such as *Cynodon* as well as taller grasses like *Panicum*, *Setaria*, *Themeda* and *Hyparrhenia* species. During the dry season elephants select the leaf bases and roots of genera including *Andropogon*, *Cymbopogon Hyparrhenia* and *Setaria*, kicking tussocks free of the ground with their feet with leaves and stems being discarded uneaten (Fig. 3.1) (Field 1971; Field & Ross 1976; Lewis 1986).

When browsing during the wet season, African elephants strip leaves,

Table 3.1. *Grass: browse proportions in the diet of African elephants in different regions*

<table>
<tr><th>Area</th><th>Method</th><th>Season</th><th>Graminoids (%)</th><th>Forbs (%)</th><th>Woody plants (%)</th><th>Reference</th></tr>
<tr><td><i>Uganda</i></td><td></td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td>Murchison Falls</td><td>Stomach contents</td><td>Wet</td><td>97</td><td colspan="2">3</td><td>1</td></tr>
<tr><td></td><td></td><td>Dry</td><td>95</td><td colspan="2">5</td><td></td></tr>
<tr><td>Queen Elizabeth</td><td>Fecal contents</td><td>Wet</td><td>90.5</td><td colspan="2">9</td><td>1</td></tr>
<tr><td></td><td>Feeding time</td><td>Wet</td><td>59</td><td>30</td><td>11</td><td>1</td></tr>
<tr><td></td><td></td><td>Dry</td><td>66</td><td>18</td><td>16</td><td></td></tr>
<tr><td>Kidepo</td><td>Feeding time</td><td>Wet</td><td>57</td><td>22</td><td>21</td><td>2</td></tr>
<tr><td></td><td></td><td>Dry</td><td>28.5</td><td>13</td><td>59</td><td></td></tr>
<tr><td></td><td>Fecal contents</td><td>Wet</td><td>73</td><td colspan="2">27</td><td>2</td></tr>
<tr><td></td><td></td><td>Dry</td><td>66</td><td colspan="2">34</td><td></td></tr>
<tr><td><i>Tanzania</i></td><td></td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td>Ruaha</td><td>Feeding time</td><td>Wet</td><td>66</td><td>9</td><td>25</td><td>3</td></tr>
<tr><td></td><td></td><td>Dry</td><td>2.5</td><td>2</td><td>92</td><td></td></tr>
<tr><td><i>Zimbabwe</i></td><td></td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td>Sengwa</td><td>Feeding time</td><td>Wet</td><td>39</td><td>—</td><td>16</td><td>4</td></tr>
<tr><td></td><td></td><td>Dry</td><td>7</td><td>—</td><td>32</td><td></td></tr>
<tr><td><i>Zambia</i></td><td></td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td>Luangwa</td><td>Feeding time</td><td>Dry</td><td>31</td><td>0</td><td>62</td><td>5</td></tr>
</table>

Source references: 1 – Field 1971; 2 – Field and Ross 1976; 3 – Barnes 1982; 4 – Guy 1976a; 5 – Lewis 1986.

Fig. 3.1 African elephants kicking out grass plants with their feet (Luangwa Valley, Zambia).

and break off branchlets to consume the terminal twigs (Fig. 3.2). Bark may be stripped by drawing small branches through the mouth. From *Acacia* trees the woody material ingested outweighs the foliage. In the Serengeti elephants obtain most of their browse from drainage line thickets, and make relatively greater use of forbs in more open habitats. In some areas small woody plants less than 1 m in height are ignored, while in other areas they are uprooted and eaten whole. When feeding on thorny *Acacia xanthophloea* scrub, elephants flatten the thorns between a tusk and the base of the trunk, and may bite off and discard the more prickly distal end (Croze 1974a and b).

In the dry season elephants feed more on bark, woody stems and roots. Bark stripping commonly occurs just before trees flower or leaf out, i.e. when the bark is likely to be rich in sap. Burning of grasslands may cause elephants to exert greater pressure on trees, but animals tend to move out of burnt areas to concentrate their feeding in unburnt marshes or evergreen forest patches. Under severe drought conditions wood, bark and roots may occupy 70–80% of the feeding time. When pressed for food animals also feed on the soft, pithy stems of trees such as baobab (*Adansonia digitata*) and chestnut (*Sterculia* spp) trees, eventually destroying the plant.

Fig. 3.2 African elephant browsing on mopane foliage (Luangwa Valley, Zambia).

Favored genera of trees and shrubs include *Acacia*, *Azima*, *Baphia*, *Brachystegia* (certain species only), *Combretum*, *Colophospermum*, *Terminalia* and *Uapaca*. Genera eaten rarely or not at all include *Boscia*, *Burkea*, *Capparis*, *Diospyros*, *Melia* and *Protea*. When feeding on *Colophospermum mopane*, elephants prefer to browse regrowth from previously damaged trees. In the dry season they discard the resinous leaves of mopane and *Commiphora* and consume woody branchlets, bark and roots (Anderson & Walker 1974; Barnes 1982a; Buss 1961; Croze 1974a; Douglas-Hamilton 1972; Field & Ross 1976; Guy 1976a; Jachmann & Bell 1985; Laws, Parker & Johnstone 1975; Lewis 1986; Napier, Bax & Sheldrick 1963; Pienaar, van Wyk & Fairall 1966b; Western & Lindsay 1984; Williamson 1975a).

In Zimbabwe 70% of all browsing occurred below a level of 1.2 m, while in Malawi the preferred feeding level was about 1.5–2 m above ground. The maximum feeding reach with the trunk is about 6 m, and trees taller than 6 m may be pushed over bringing higher branches within reach. However, elephants do not always feed on trees they have felled. In Zimbabwe elephant bulls pushed over, as a year-round average, 6 trees per day, compared with 2.6 per day by cows. In Serengeti in Tanzania the tree pushing rate by bulls averaged only 0.7 per day, and only 30% of tree pushing attempts were successful, trees greater than about 0.25 m in diameter commonly withstanding attempts to push them over. The rate of food intake obtained from the herb layer is considerably higher than that secured from pushed over trees. Trees pushed over in the Kasungu National Park in Malawi showed a height mode of 4–5 m for favored species, but 2–3 m for species generally rejected as food. Since pushed over trees commonly coppice from the base, this selective damage could lead to increased availability of food at an accessible feeding level (Croze 1974a; Guy 1976a; Jachmann & Bell 1985).

Elephants feeding in forest patches in Uganda are attracted to regeneration in the patches opened by timber management. They favor stems under 250 mm in diameter and commonly break off leader shoots, thereby maintaining the secondary growth. Important timber species such as *Khaya* (mahogany), *Chrysophyllum*, *Cordea* and *Maesopsis* are favored as food, so that the course of forest succession is deflected to less desirable species (Laws 1970; Wing & Buss 1970). In Ivory Coast, elephants do most of their feeding in secondary rain forest, but depend on primary forest for certain fruiting trees (Merz 1981).

The daily food intake of African elephants has been estimated either from the mass of the stomach contents, assuming a mean turnover time of 12 hours; or by extrapolating from the feeding rate and daily feeding time. Both methods give similar results, indicating a mean daily food intake of about 1.0–1.2% of body mass per day for males and non-lactating females, and 1.2–1.5% of body mass per day for lactating females (dry mass/livemass). Food intake appears somewhat higher in the wet season than in the dry season on a wet mass basis, but the difference would probably be reduced if measured as dry mass. Crude protein concentrations in the stomach contents of elephants culled in Uganda varied between 6% and 14% during the wet season, and 5% to 8% during the dry season. Animals from the Queen Elizabeth Park, where there was a higher proportion of browse in the diet, showed higher protein contents than animals from the Murchison Falls Park, where the diet consisted mostly of grass (Guy 1975; Laws, Parker & Johnstone 1975; Malpas 1977; McCullagh 1969).

African elephants defecate about 14–20 times per day in the wet season, and about 10 times per day during the dry season. An adult produces between 6 kg and 11 kg of feces per defecation on average, depending on its size. On average, the total quantity of feces produced per day would amount to about 150 kg wet mass, or 35 kg dry mass. If the daily food intake of an adult male is about 60 kg dry matter per day, this suggests a dry matter digestibility of about 40% (Barnes 1982a; Coe 1972; Dougall & Sheldrick 1964; Guy 1975; Wing & Buss 1970; Wyatt & Eltringham 1974).

Asian elephants devoted 89% of their feeding time to grass in the Ruhunu Park in Sri Lanka; while in the Gal Oya Park, also in Sri Lanka, grass formed just over 50% of the diet. Even in the forests of Malaya, grass occupied up to one third of feeding time. Most of the grass eaten consisted of short grasses, entire plants being consumed. Grass plants shorter than about 60 mm were kicked out of the ground with the feet, then gathered with the trunk. Tall swamp grasses were eaten during the winter dry season. Availability of freshly growing grass seemed to be the main factor controlling seasonal movements.

At Ruhunu, elephants foraged preferentially in open scrub or scrub-forest, and made relatively little use of evergreen forest vegetation. Gap-colonizing species of woody plant were favored over shade-tolerant species. In both areas in Sri Lanka, utilization of woody plants was largely by branch breaking, foliage plus bark being stripped from the broken off stem. Plants with a stem girth between 20 and 160 mm were favored. The rarity of bark stripping from main stems may be due to the lack of tusks in most of the elephants observed. Tree pushing was also rare. Small woody plants were commonly eaten whole. With spiny shrubs the trunk was drawn up the stem to flatten the spines before plucking. In Malayan forests elephants eat mostly quick growing pioneer species, and the dominant trees of the Dipterocarpaceae are rejected. Favored feeding areas in forest regions are the open glades bordering rivers (McKay 1973; Mueller-Dombois 1972; Olivier 1982; Vancuylenberg 1977).

Asian elephants defecate between 12 and 18 times per day in the wild. A captive adult male fed hay produced 114 kg (wet mass) of feces per day (Benedict 1936; Vancuylenberg 1977).

Hippopotamus

Hippos are area selective grazers with a preference for short green grass. Grasses and sedges form 95–99% of the food eaten by hippos in different regions, the remainder being made up by forbs, which increase in representation during the dry season. Short or leafy species of grass are favored, and coarser grasses tend to slip between the lips and so are neglected. Favored genera include *Panicum*, *Cynodon*, *Brachiaria*, *Sporobolus*, *Themeda*, *Digitaria*, *Heteropogon*, *Urochloa*, *Hemarthria*, *Echinochloa* and *Cyperus*, based on observations made in Uganda, Zaire and Natal. Aquatic herbs such as *Pistia* are eaten in small quantities. The large pods of *Kigelia* are reportedly eaten in Zambia.

Hippos pluck grass close to ground level, and their feeding promotes the development of short grass lawns bordering the pools serving as their daytime refuges. Most feeding occurs within a kilometer or less of water during the wet season, but in the dry season animals may move 2–3 km or more from rivers or lakes (Field 1970; Lock 1972; Mackie 1976; O'Connor & Campbell 1986; Olivier & Laurie 1974; Scotcher, Stewart & Breen 1978).

A hippo's stomach contents amount to 13–15% of body mass on a wet mass basis and represent two nights feeding. Estimated daily food intake on a dry mass basis is 1.1% of body mass for males and 1.3% for females, with lactating females having higher stomach fills than pregnant females (Laws 1968b).

Giraffe

Giraffe are almost exclusively browsers, feeding on the leaves and shoots of trees and shrubs. Herbaceous material, including climbers, vines and taller forbs (but no grass), forms between 0.2% and 7% of the year-round diet in different areas. Flowers, fruits and pods are favored when available. Females consume a higher proportion of herbaceous plants than males.

Giraffe favor deciduous trees and shrubs during the wet season, but rely increasingly on evergreen or semi-evergreen species as the dry season advances. During the late dry season their feeding tends to be concentrated in the forest or thicket fringes flanking rivers and dry watercourses. Important food genera include *Acacia*, *Capparis*, *Combretum*, *Kigelia*, *Securinega* and *Ziziphus* during the wet season, and *Albizia*, *Balanites*, *Boscia*, *Colophospermum*, *Diospyros*, *Euclea*, *Grewia* and *Melia* during the dry season. Favored fruits include the pods of various leguminous trees, the huge woody pods of *Kigelia* (Fig. 3.3), and hard baseball sized fruits of *Gardenia* and *Strychnos* (Field & Ross 1976; Hall-Martin 1974; Kok & Opperman 1980; Leuthold & Leuthold 1972; Lightfoot 1978; Pellew 1984b; Sauer, Theron & Skinner 1977).

Giraffe seek out the new unhardened shoots of *Acacia* species, and their feeding stimulates increased shoot production by these plants. From hardened shoots they strip leaves from branch ends with their tongues, or bite off the shoot end. The proportion of woody material ingested increases in the dry season, forming 15% of the rumen contents at this time, compared with 5% during the wet season. At Tsavo in Kenya giraffe performed 67% of their feeding below 2 m during the wet season, decreasing to 37% during the dry season; but at Kyle in Zimbabwe only 20% of feeding was below 2 m. At Serengeti in Tanzania bulls did 75% of their feeding above

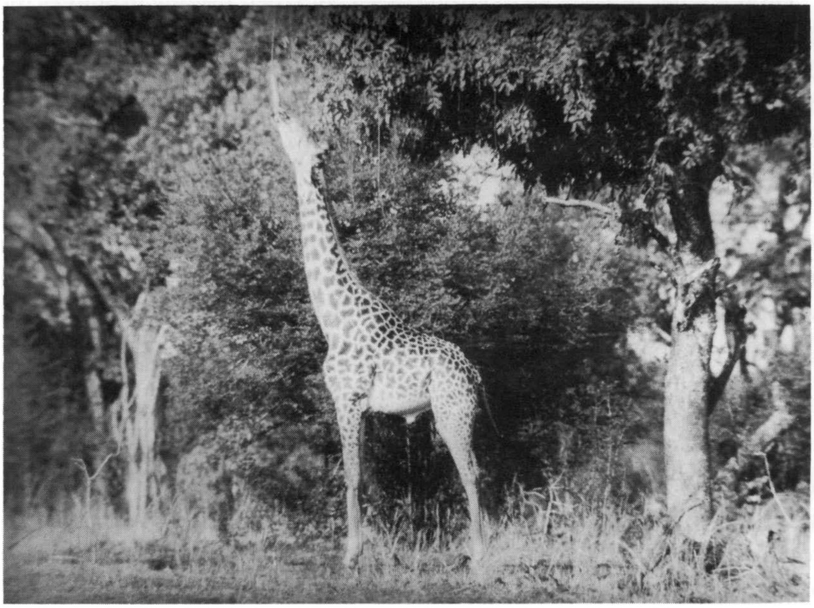


Fig. 3.3 Giraffe plucking the large woody pod of *Kigelia pinnata* (Luangwa Valley, Zambia).

4 m, while for cows 78% of feeding was done below 3 m (Leuthold & Leuthold 1972; Lightfoot 1978; Pellew 1983a, 1984b).

Based on feeding rate and daily feeding time, the food intake of giraffe is estimated to be 2.1% of body mass for females, and 1.6% for males, on a dry mass basis. The crude protein content of the material in the rumen varies between about 19% in the wet season and 14.5% in the dry season for adult females, with values for adult males being about 3–4% lower (Field & Blankenship 1973; Hall-Martin & Basson 1975; Pellew 1984c).

Rhinoceroses

For Indian rhinos in Nepal, tall canelike grass species form the main food source year-round, in particular species of *Saccharum*. These are most favored when young in spring. Short grasses, such as *Cynodon*, and herbs make up the bulk of the diet during the monsoon period, with aquatic herbs such as *Ceratophyllum* and *Hydrilla* especially favored. Woody browse forms about 2.5% of the diet during the monsoon, increasing to 22% during the winter period. Fallen fruits are also eaten. When grazing on short grasses, Indian rhinos fold back the projecting upper lip (Laurie 1982).

Sumatran rhinos in the Gunung Leuser Park in Sumatra feed mainly on

Fig. 3.4 Black rhino browsing on low *Acacia* scrub (Umfolozi, South Africa).

small trees or saplings, consuming twigs, small branches and leaves, and also certain fruits. Herbs and lianas formed only 1% of the plants recorded as eaten. To reach the higher shoots of woody saplings, animals bend or break the stem by walking over the plant and pressing down on the trunk with the body. Sumatran rhinos snapped with ease plants with stem diameters of up to 50 mm (Borner 1979). Javan rhinos are also browsers, feeding mainly on the twigs and branches of saplings (Schenkel & Schenkel-Hulliger 1969b).

Black rhinos are predominantly ground feeders, concentrating on forbs and low-growing woody scrub (Fig. 3.4). Grass occupies no more than 1–5% of the feeding time even in open grassland habitats such as Ngorongoro Crater, Tanzania, and Masai Mara Park, Kenya. In the semi-arid steppe of Tsavo East National Park, Kenya, grasses were unrepresented in feeding records. Forbs and dwarf shrubs, especially legumes such as *Indigofera*, *Tephrosia*, *Trifolium*, *Lathyrus*, *Aeschynomene*, and *Caesalpinia*, are the favored food source, and occupy between one third and three-quarters of feeding time during the wet season.

Woody browse becomes more important in the diet following fires which remove the herb layer. Woody plants are also relatively more important in

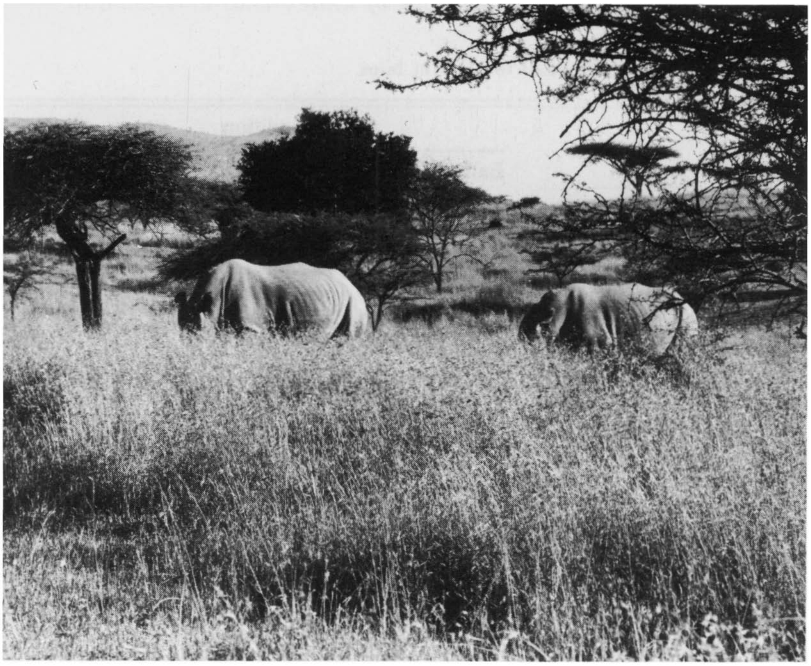


Fig. 3.5 White rhino grazing short grass (Umfolozi, South Africa).

Namibia and at Addo in the southern Cape where herbs are less plentiful. When browsing the prehensile upper lip is used to pull twigs into the mouth, and these are then bitten off with the molars. The preferred browsing level is between 0.5 and 1.2 m, with the maximum reach being 1.5 m. Black rhinos bite off shoot ends 100–250 mm in length and up to 10 mm in thickness, and may consume 30–60% of the above-ground biomass of plants under 0.5 m in height. Species lacking thorns may be defoliated by running the lips over the twigs. Important food sources include genera such as *Acacia*, *Combretum*, *Croton*, *Dichrostachys*, *Grewia* and *Terminalia*. Common woody species rejected as food at Tsavo include *Boscia*, *Commiphora* and *Dobera*. *Colophospermum mopane* is eaten in limited amounts during the wet season in Namibia. Stem succulents such as species of *Euphorbia* become an important food source during the dry season if available. At Tsavo such plants formed up to 70% of the food intake despite their high latex content. Woody plants generally increase in representation in the dry season. During the hot, dry mid-summer period at Addo, leaf succulents such as *Portulacaria* made up over 40% of the food. The horns may be used to break down higher branches, with main stems up to 170 mm in diameter being snapped. Bark may also be stripped from certain species, for example

Table 3.2. *Trends in the food selection of white rhinos in relation to grassland condition*

Figures represent percentage of total plant bites.

	Grass condition					
Grass form	Early green[a]	Late green	Mainly green	Mainly brown	Brown	Year[b]
Short grass species	56.9	54.7	45.4	20.0	18.3	46.3
Climax grass species	26.8	23.9	27.2	56.5	66.6	33.4
Shade grass species	10.4	16.9	17.3	18.8	7.8	13.8
Miscellaneous grass species	4.8	4.2	7.4	2.0	5.2	5.3
Sedges	0.2	0.6	0.4	0	0.8	0.2
Forbs	0.7	0.2	1.9	3.7	1.3	1.0
Mean grass height (leaf table, mm):						
Before grazing	75	130	100	170	240	
After grazing	30	55	35	60	110	
N (total plant bites)	1634	2230	988	249	1002	6103

Notes: [a] Pre December 31.
[b] Weighted mean.

Euphorbia tirucalli (Goddard 1968, 1970a; Hall-Martin, Erasmus & Botha 1982; Hitchins 1979; Joubert & Eloff 1971; Mukinya 1977).

Black rhinos defecate 4–5 times in 24 hours. Coprophagy has been recorded during the dry season when legumes were sparsely available (Goddard 1968; Joubert & Eloff 1971).

White rhinoceros. To determine the diet composition of white rhinos, I observed feeding animals at close quarters (20–40 m range), and then inspected the feeding site after the animal had moved on. Within an area defined by what I could touch with my fingers while standing with legs straddled, I counted the number of plants of each species that had been freshly grazed. A unit plant was defined by the spread between my extended middle finger and thumb, which distance closely approximates the measured bite width of a white rhino (200 mm). Feeding records were divided according to the general grass condition, in terms of its greenness at the time of grazing, as influenced by prior rainfall.

Short grasses were the most important food source during the wet season while the grass remained green or mainly green (Fig. 3.5, Table 3.2). Favored short grass species included *Panicum coloratum*, *Urochloa mosambicensis*, *Digitaria* spp and *Sporobolus* spp. Shade grasses, in particular *Panicum maximum*, were sought out especially during the early dry season, when they tended to remain green longer than other grasses. During

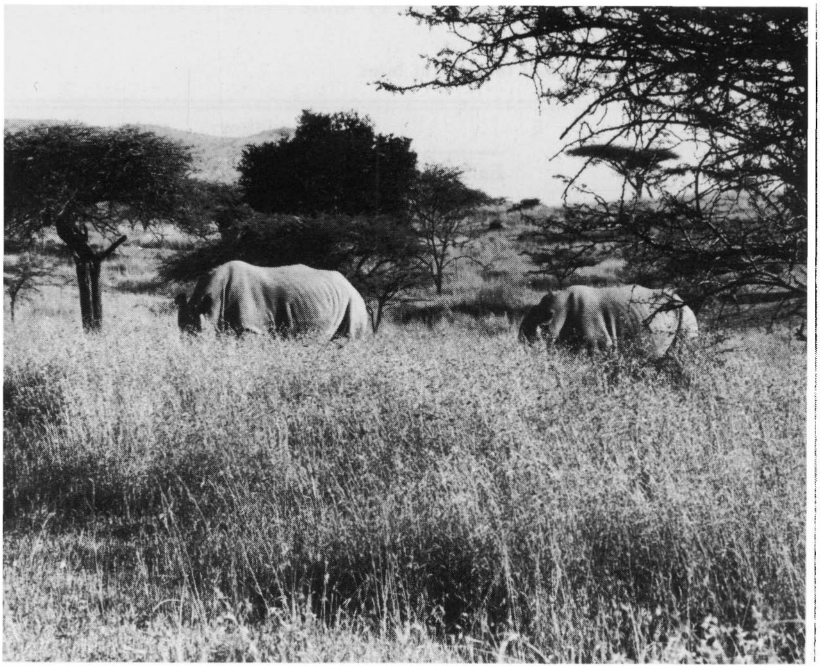


Fig. 3.6 White rhino grazing in medium-tall *Themeda* grassland during the dry season (Umfolozi, South Africa).

the dry season rhinos transferred their attention increasingly to medium-tall climax grassland dominated by *Themeda triandra* (Fig. 3.6). *T. triandra* was also favored during the wet season when kept short. This species provided the greatest fraction (about 30%) of the food intake on a year-round basis. The only grasses that were strongly rejected were *Cymbopogon* spp (which are aromatic), *Aristida* spp (which are wirey), and *Tragus berterionanus* (which is a very low-growing annual). However, another aromatic species, *Bothriochloa insculpta*, was readily eaten, at least when short. Forbs made up only 1% of the annual diet, and seemed mostly to be ingested accidentally along with grass. No browsing was observed, apart from occasional instances of chewing on woody stems.

White rhinos selected mainly for grassland type, rather than for particular grass species. During the wet season months they concentrated their grazing on short grass grasslands (Fig. 3.7). As the dry season advanced, they shifted their grazing to areas of medium-tall *Themeda* grassland, though initially seeking out patches of short grass. The fringe of short grass associated with termite mounds was especially favored. By the end of the

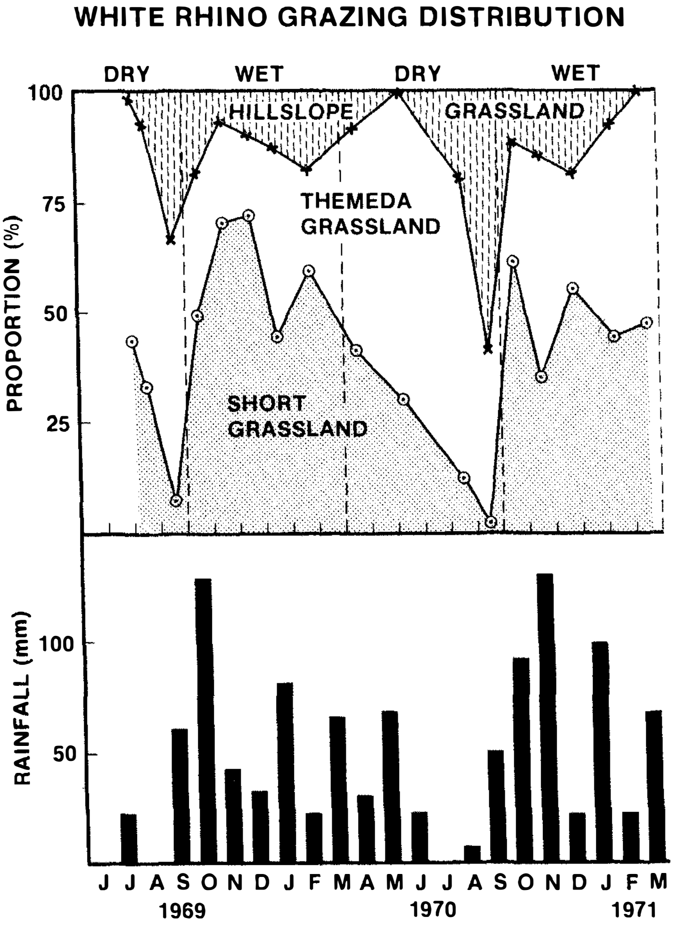


Fig. 3.7 Seasonal changes in the distribution of grazing white rhinos between different grassland types in the western section of Umfolozi Game Reserve.

dry season most of the *Themeda* grassland on gentle terrain had been grazed down, and animals then moved up onto hillslopes to graze remaining reserves of taller grassland.

While grazing, white rhinos swung the head in an arc to crop the grass that came within reach with each forward step. The mean height of the grass grazed increased from about 100 mm during the wet season to about 200 mm during the dry season. This was cropped down to a height of 25–60 mm except when tall dry grass was being eaten (Table 3.2). On short grass the feeding rate averaged 72 bites per minute.

Soil type also influenced grassland selection. White rhinos favored areas of grassland growing on soils derived from shale or dolerite, but were rarely seen grazing in areas underlaid by sandstone. The mean crude protein content in whole plant samples of *Themeda triandra* growing on sandy soils in Umfolozi was 5.9%, compared with 7.8% for plants of the same species collected from bottomland sites with clayey soils. *Panicum maximum* showed a similar difference (11.7% versus 14.9%; Downing 1979).

The prevalence of short grass grasslands at Umfolozi is largely due to the grazing effects of white rhinos. With sustained close cropping, erect tufted species like *Themeda* lose vigor and become replaced by short creeping species like *Panicum coloratum*, *Urochloa* spp, *Sporobolus smutsii* and *S. nitens* (Downing 1972).

In the Hluhluwe Reserve medium-tall grasslands predominate, mostly underlaid by sandstone or granite. White rhinos sought out short grass patches, the favored grass species in such habitats being *Dactyloctenium australe*. White rhinos introduced from Umfolozi into the Matopos Park in Zimbabwe, where granitic sands predominate, likewise favored mostly short grass species (Wilson 1969b). I made some brief observations on the white rhinos held in a 250 ha enclosure in the Pretorius Kop region of the Kruger Park in South Africa, also a sourveld region underlaid by granite. The predominant grass species eaten were *P. maximum*, *Setaria perennis*, *Cynodon dactylon*, *U. mosambicensis* and *Digitaria* spp, under wet season conditions. No use was made of the tall *Hyperthelia* and *Cymbopogon* predominating in parts of the enclosure.

White rhinos of the northern subspecies were recorded in Uganda feeding mainly on medium-height grasses, including *Hyparrhenia*, *P. maximum*, *Chloris gayana*, *Heteropogon contortis* and *Brachiaria brizantha*. The general height of the grass cropped was 250–300 mm, this being reduced to a level of about 50 mm (Foster 1967; van Gyseghem 1984).

I had one opportunity to weigh the stomach contents of a white rhino cow, which had died of acute peritonitis. The wet mass of the food material in the stomach was 72 kg, equivalent to about 4.5% of body mass. What proportion of the daily food intake this represents is unknown. The defecation rate of bulls varied betwen 4 and 6 times per 24 hours, based on monitoring the dungheaps used regularly by these individuals.

Summary

Both African and Asian elephants are mixed feeders, favoring grass when it is green, but becoming more dependent on woody browse in the dry season. Furthermore elephant diets vary flexibly between different regions depending on the relative availability of grasses and woody plants.

The dry season food intake may include a high proportion of fibrous plant tissues such as twigs, bark and roots. Nevertheless, high quality plant parts such as fruits are sought out when they are available. Elephants tend to reject shade-tolerant, late succession species in forest habitats. They also ignore some savanna species eaten readily by giraffe (e.g. *Melia volkensii* at Tsavo). The high defecation rate suggests a fast turnover of food in the digestive tract.

Indian rhinos are also mixed feeders, but generally favor grass. Both tall and short grass species are eaten. Indian rhinos are dependent upon flood plain areas where some green growth remains available year-round, although the proportion of browse in the diet increases in the dry season.

Both white rhino and hippo are strictly grazers, including no woody browse in their diets. They are generally area selective rather than species selective grazers. Both favor short grasses, but can switch to taller relatively fibrous grassland when short grass in unavailable. However grasslands growing on nutrient-poor soils tend to be avoided.

Black rhino, Javan rhino, Sumatran rhino and giraffe are browsers, including only small amounts of grass in the diet. Black rhinos favor herbaceous browse (forbs), but become more dependent on woody plants and succulents during the dry season. Giraffe and other browsing rhinos favor the new shoots of woody trees or shrubs. Fruits and pods are sought out when available.

Water and other habitat needs

The water requirement of herbivores may be largely met from the liquid content of plant tissues, plus water released during carbohydrate metabolism. Nevertheless, these sources may prove inadequate at certain times of the year, so that the liquid intake may need to be supplemented by drinking from standing surface water.

Body liquid balance becomes especially important in thermoregulation, when animals may become dependent upon evaporative cooling. Heat loads may also be avoided or reduced by behavioral responses, such as seeking shade or wallowing in water or mud. Animals may also need to restrict heat losses during cold or windy weather by seeking shelter in protected sites.

Certain minerals, in particular sodium, may be present in inadequate amounts in the diet, and may be sought out at sites where such minerals have become concentrated in soil.

Fig. 3.8 Elephants wallowing in a muddy pool (Mana Pools, Zimbabwe).

Elephants

African elephants drink one to three times daily when water is readily available. During the dry season they may go for periods of two or three days between waterhole visits, but remain dependent on regular access to surface water. In the Hwange Park in Zimbabwe, where soils are sandy and leached of minerals, pools with relatively high sodium contents are favored for drinking (Eltringham 1982; Laws 1970; Weir 1972; Wyatt & Eltringham 1974).

Surface water availability restricts the dry season distribution of elephants. At Tsavo in Kenya, elephants were restricted to a radius of about 15 km from water under conditions where they were dying from starvation. However at Hwange elephants undertook journeys of up to 24 km to and from water during a drought (Corfield 1973; Williamson 1975a).

Elephants lie and roll over in muddy pools (Fig. 3.8), and immerse themselves in deeper bodies of water. They use their trunks to spray water or mud over their bodies, and sometimes also blow dusty soil over themselves. After mud wallows they frequently rub themselves against trees (Hendrichs 1971; personal observations).

Elephants seek shade during the hot time of the day, with groups clustering under the remaining large trees where woodlands have been depleted. The enormous ear pinnae of African elephants facilitate cooling. Ear fanning rates are correlated with ambient temperature, and the temperature of the blood leaving the ear is cooler than that of the blood entering it (Buss & Estes 1971).

African elephants dig up and eat sodium-rich soil in saline depressions in Hwange. At one site in Kenya they penetrate into the deep recesses of a cave for the salt deposits there (Weir 1972).

Asian elephants usually drink one or more times daily. Males commonly lie and roll in muddy hollows, while females more often collect muddy liquid in their trunks and spray it over their bodies. Mud and dust is also collected in the curled trunk and thrown over the body, frequently after bathing in water. This may be followed by rubbing the skin against suitable trees or rocks (McKay 1973).

Hippopotamus

Hippos generally spend the daytime largely submerged under water, thereby avoiding heat stress. Sun basking on sandbanks may take place during the cooler winter period.

Giraffe

Giraffe can survive independently of surface water for long periods if adequate green foliage is available on trees, but drink regularly when water is readily available. Giraffe do not immerse themselves in water or mud. They may continue feeding through the midday period without seeking shade (J. T. du Toit personal communication 1986; Foster & Dagg 1972; Western 1975; personal observations).

Rhinoceroses

Indian rhinos drink daily, and ingest mineral-rich soil when it is available. They spend long periods lying in pools of water, especially during the hot summer months (Ullrich 1964; Laurie 1978; Fig. 3.9). Both Javan rhinos and Sumatran rhinos commonly wallow in muddy pools (Hubback 1939; Schenkel & Schenkel-Hulliger 1969b; Borner 1979).

At Hluhluwe, where water is widespread, black rhinos generally drink nightly. In Namibia, black rhinos drink every second night during the cool dry season months of June–July, but nightly during the hot dry month of October. However, in the Tsavo East Park in Kenya, black rhinos went for periods of 4–5 days without drinking.

Black rhinos commonly wallow in mud, and sometimes also in dust

Fig. 3.9 Indian rhino lying in a pool (Chitwan, Nepal, photo courtesy W. A. Laurie).

hollows. The favored time for mud wallowing is the late afternoon, but wallowing also occurs at night. Animals commonly rub against bushes or rocks following wallowing. Salt licks are commonly visited (Frame 1971; P. M. Hutchins personal communication; Joubert & Eloff 1971; Mukinya 1977; Schenkel & Schenkel–Hulliger 1969a).

White rhinoceros

At Umfolozi water was abundantly available in numerous small depressions or pans during the wet season. White rhinos then drank daily, or even twice daily. During the dry season after these pools had dried up, animals were forced to make a journey to one of the longer-lasting pools or to one of the major rivers. To determine the frequency of drinking at this time of the year, I used three sets of evidence: (i) movements of those animals fitted with radio transmitters; (ii) identities of the animals drinking at particular waterholes on successive days; (iii) relationships between the interval between waterhole visits and the time spent drinking. Results showed that a drinking frequency of every 2–3 days was most usual during the dry season period, although some animals drank at four day intervals.

Wallowing also took place at waterholes, and took two different forms. Animals lay down and rolled in muddy hollows to secure a thick coating of glutinous mud over the body. Following a mud wallow, animals rubbed their bodies against suitably inclined trees, stumps or rocks in the vicinity

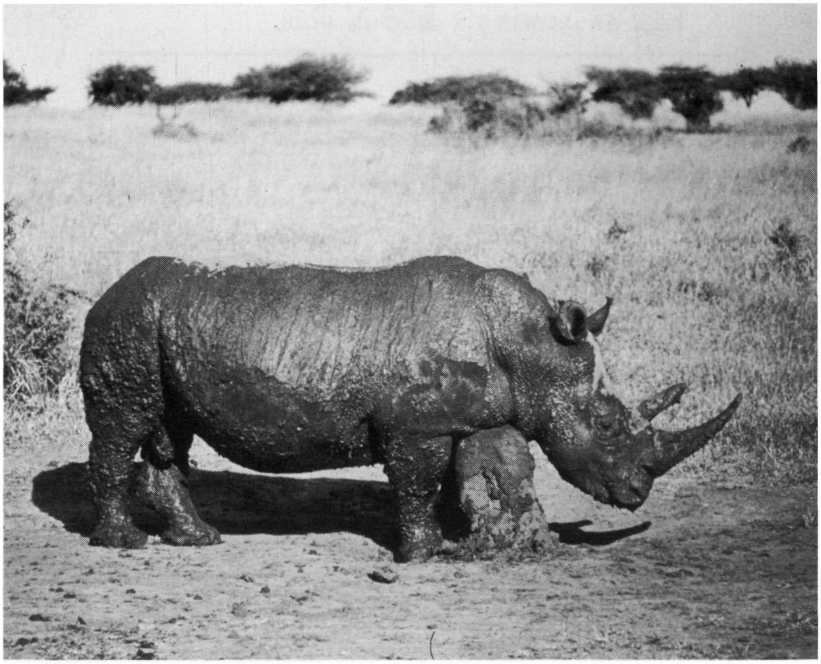


Fig. 3.10 White rhino bull rubbing mud-plastered body against a stump (Umfolozi, South Africa).

(Fig. 3.10). Ticks were evident in the mud rubbed off. Animals also at times lay down in pools of water, for periods of up to several hours.

Mud-wallowing occurred most frequently in the early afternoon, but was recorded at all times of the day and even during the night. Lying in water was most common over midday, but on occasions took place even during the coolest part of the early morning (Fig. 3.11). Lying in water was much more common during the earlier part of the wet season than during the later part, while mud-wallowing was recorded equally frequently in both of these periods. Little wallowing took place during the dry season months, even when suitable mud was available.

During the heat of midday, white rhinos sought out suitably shady trees. Animals tended to congregate at favored sites, generally located on breezy ridgecrests. Under cool, windy conditions, white rhinos secluded themselves in lowlying areas of woodland or thicket.

No saltlicks were known to me in Umfolozi. However the water issuing from springs tended to be brackish. A few instances of animals licking termite mounds were noted.

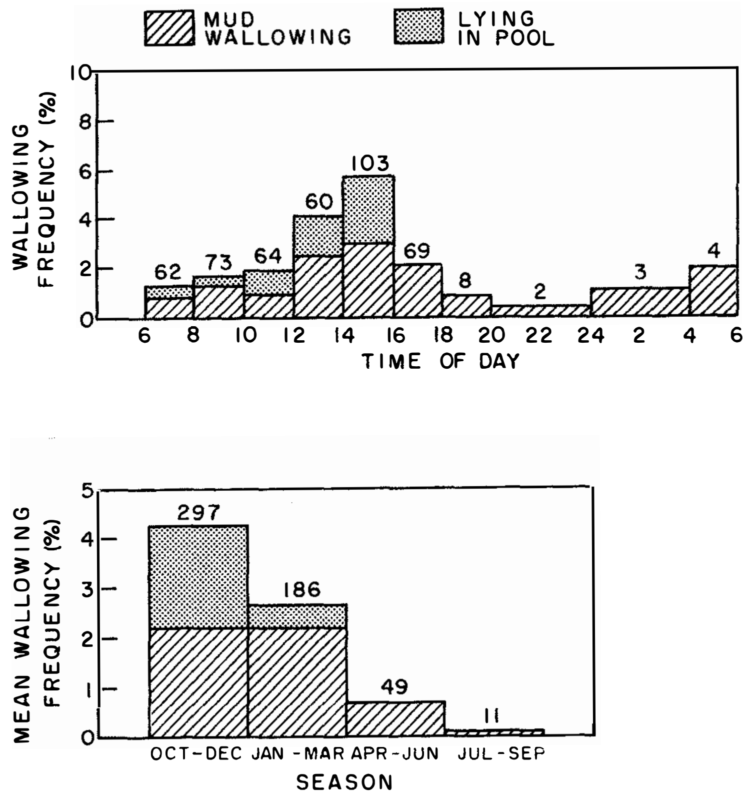


Fig. 3.11 *Wallowing frequency of white rhinos in relation to time of day and season.*

Summary

Hippos, Indian rhinos and elephants are strongly dependent on surface water availability, while white rhinos and black rhinos can go for periods of several days without water. Giraffe can be independent of water if green foliage remains available. Hippos are aquatic by day, while elephants and rhinos wallow both in water and mud. Giraffe do not wallow. All species except giraffe are shade-dependent over the midday period.

Comparisons with smaller ungulates

Megaherbivores show distinctions between grazers, browsers and mixed grazer-browsers as is typical among African bovids. White rhinos and hippos are as strict grass-feeders as African buffalo, wildebeest and topi. Black rhinos include no more grass in their diet than browsing antelopes like kudu, bushbuck and Grant's gazelle (although the term 'concentrate selector' can hardly be applied to black rhinos). Elephants and Indian rhinos switch between a primarily graminoid diet in the wet season, and increased representation of woody browse in the dry season, like impala, Thomson's gazelle and, to a lesser degree, eland; but, like impala in particular, elephants of both species show a wide regional variation in grass: browse proportions (Hofmann & Stewart 1972; Owen-Smith 1982).

Megaherbivores seek out the same high quality plant parts as those selected by smaller ungulates. White rhinos and hippos favor leafy short grasses, as do wildebeest, impala and warthog. Elephants, browsing rhinos and giraffe seek out seed pods and other fruits when available, as do most browsers from dikdik size upwards; while giraffe search for new unlignified shoots, as do duikers. Black rhinos favor legumes and other herbaceous browse, like kudus. However, megaherbivores include in their diets a higher proportion of stem and other fibrous tissues than do smaller ungulates, most particularly during the dry season period. In their consumption of bark and woody twigs megaherbivores are paralleled by small cecalids, such as African porcupine and hares (Bryant *et al.* 1985; Jarman 1974; van Jaarsveld & Knight-Eloff 1984).

Megaherbivores tend to favor the same species of plant as those sought out by smaller ungulates. However, African elephants make abundant use of *Colophospermum mopane*, which is eaten by giraffe and browsing antelopes such as eland and kudu only in the late dry season when little choice is available; while the *Brachystegia* species that elephants eat are also little used by other browsers. Hippos commonly graze *Sporobolus pyramidalis* in Uganda, a coarse tall grass which is generally avoided by other grazers. White rhinos in Zululand readily eat *Bothriochloa insculpta*, a strongly aromatic grass species, at least while it is young, although grazing antelope ignore this species unless hard pressed for food. Certain very large fruits, in particular the woody pods of *Kigelia pinnata*, are eaten only by giraffe and black rhinos.

All megaherbivores except giraffe are dependent upon the availability of surface water, like most antelope species except for many of the browsers. However white rhinos are able to go for longer periods between drinking than most grazing bovids and zebras under dry season conditions when no green grass is available (Western 1975).

Mud-wallowing and bathing in pools are habits shared by elephants, rhinos and hippos with other ungulates having relatively hairless skins, for example African buffalo, water buffalo and warthog. While some hairy ungulates also wallow in muddy hollows, for example American bison and red deer, this behavior is restricted to males during the rutting season

(Cumming 1975; Darling 1937; Eisenberg & Lockhart 1972; Lott 1974; Sinclair 1977; Struhsaker 1967).

Megaherbivores, apart from giraffe, seem similarly shade-dependent to most medium-sized ungulates, although some of the latter are able to spend long periods exposed to full sunlight due to their protective hair coats (Finch 1972).

4

Space–time patterns of habitat use

Introduction

In this chapter I consider how megaherbivores go about securing their habitat requirements in time and space. What times of day or night are favored for feeding or other maintenance activities, how much time per day is spent foraging, and how does this vary through the seasonal cycle? What size area do animals cover in seeking their food or water needs, and how does this change seasonally?

Temporal patterning of activities

Animals engage in a number of daily activities. These include feeding, travelling between feeding areas and perhaps to and from water, resting, other maintenance behaviors such as drinking, wallowing and grooming, and various forms of social interaction. These need to be scheduled optimally within the diel (day-night cycle), while ensuring that an appropriate amount of time is allocated to each. The animals need to accommodate for variations in temperature, cloud cover, wind and precipitation. Superimposed on these variations is the progression of the seasons, involving changes in the day-night ratio, prevailing temperatures and rainfall, and associated changes in food availability and reproductive physiology.

In the following account I will make a distinction between feeding and foraging. The former is synonymous with eating, i.e. gathering, chewing and swallowing, while the latter also includes movements made while searching for food.

Elephants

African elephants devote roughly equal proportions of the day and night to foraging. They tend to show three peaks in activity, occurring during the early morning, the later part of the afternoon, and around

Table 4.1. *Daily foraging time of African elephants in different regions*
Figures represent percentage of total time.

Area	Sex	Season	Daylight	24 hour	Reference
Uganda					
Queen Elizabeth	Female	Year	—	75	1
Tanzania					
Serengeti	Male	Year	—	75	2
Ruaha	Male	Wet	70–85	—	3
		Dry	56	—	
	Female	Wet	82	—	
		Dry	64	—	
Zimbabwe					
Sengwa	Combined	Wet	56.5[a]		4
		Dry	41.5[a]		

Note: [a] 8 hour day only.
Source references: 1 – Wyatt & Eltringham 1974; 2 – Hendrichs 1971; 3 – Barnes 1979; 4 – Guy 1976b.

midnight. Their main rest period is just before dawn when they may lie down for an hour or two. Most other resting is accomplished standing up. Most travelling takes place shortly after dusk.

The overall proportion of the 24 hour cycle devoted to foraging varies between 60% and 75% in different areas (assuming 80% of the night is devoted to foraging; Table 4.1). More time is spent foraging in the wet season than in the dry season. Elephants spend more of their time foraging in grassland areas than in woodlands. Males and females spend very similar proportions of their time foraging. Resting, whether standing or lying, occupies only 2–3 hours during the day and 1–3 hours at night; whilst travelling (i.e. walking without feeding) takes up about 2–3 hours in total (Barnes 1979; Guy 1976b; Hendrichs 1971; Wyatt & Eltringham 1974).

The peak drinking time of African elephants is during the early evening, with the majority of animals arriving at water between 18.30 and 21.00 (du Preez & Grobler 1977; Weir & Davison 1965).

Asian elephants forage for 75% of the daylight hours, or an estimated 17–19 hours per 24 (Vancuylenberg 1977).

Hippopotamus

Hippos spend the entire day resting in water, and emerge on land to forage only at night. Animals generally leave the water after nightfall and return during the early pre-dawn hours. Adult males are the last to leave, emerging from the water as late as 20.00–21.00, though somewhat earlier in dull weather. Animals begin drifting back to their pools between 02.00 and 03.00, with the majority of hippos back in the water by 04.00. This leaves no more than 7–8 hours for foraging, though after reaching their grazing areas animals feed with little pause (Verheyen 1954; personal observations).

Giraffe

Giraffe forage for most of the day, but devote much less time to foraging at night. There is also a sex difference in foraging time. At Serengeti cows foraged for 72% of the day versus 55% for bulls. The mean proportion of the night spent foraging by both sexes combined was 34% on moonlit nights and 22% on dark nights. More time was spent foraging during the dry season than in the wet season, but the time spent actually eating may be less. The main feeding periods are during the three hours post-dawn and again pre-dusk. At Kyle in Zimbabwe animals moved into patches of woodland at night, possibly because of the high concentration of browse in a small area. However, ruminating is the dominant nocturnal activity, and time is also spent lying down. Sleep periods are brief, lasting no more than 5.5 min on average. Adult males spent 5% more time walking per day than adult females (Lightfoot, 1978; Pellew, 1984c).

Giraffe have no special drinking time, and may appear at water at any time of the day or night (du Preez & Grobler, 1977; Weir & Davison 1965).

Rhinoceroses

An Indian rhino cow, watched for 24 hours in January (midwinter), spent 57% of its time foraging and 40% lying. Another cow watched for 22 hours in April (towards the end of the dry pre-monsoon period) spent 65% of its time foraging. Less time was spent foraging during the rainy monsoon season (Laurie 1978).

Black rhino females at Hluhluwe were active for 47% of the day and 95% of the night, and males for 33% of the day and 93% of the night, as indicated by radio-telemetric monitoring. In East Africa black rhinos spent 30% of the daylight hours eating and 20% walking, including movements between feeding stations. Their peak drinking time is in the early evening between 18.00 and 21.00 (du Preez & Grobler 1977; Goddard 1967; Hitchins 1971; Mukinya 1977).

White rhinoceros

I recorded the activities of all white rhinos when encountered, and maintained a continuous record of the activities of animals kept under

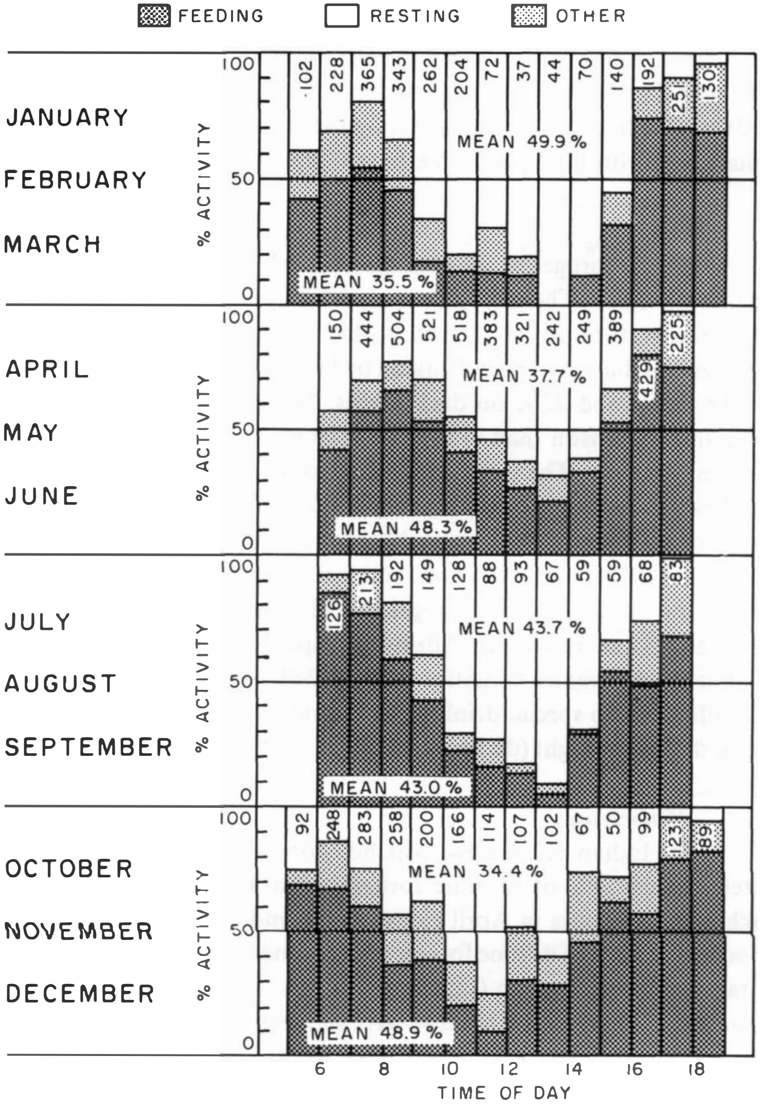


Fig. 4.1 Diurnal activity pattern of white rhinos at different seasons (for sunny days only). Figures indicate total sample sizes, in 15-min rhino activity units.

observation for extended periods. From continuous watches, the prevailing activity over each 15 min period was extracted. Brief records were assigned to the 15 min period in which they were observed. Thus records were analyzed in terms of 15-min rhino activity units.

White rhinos showed a bimodal activity pattern (Figs. 4.1 and 4.2). The

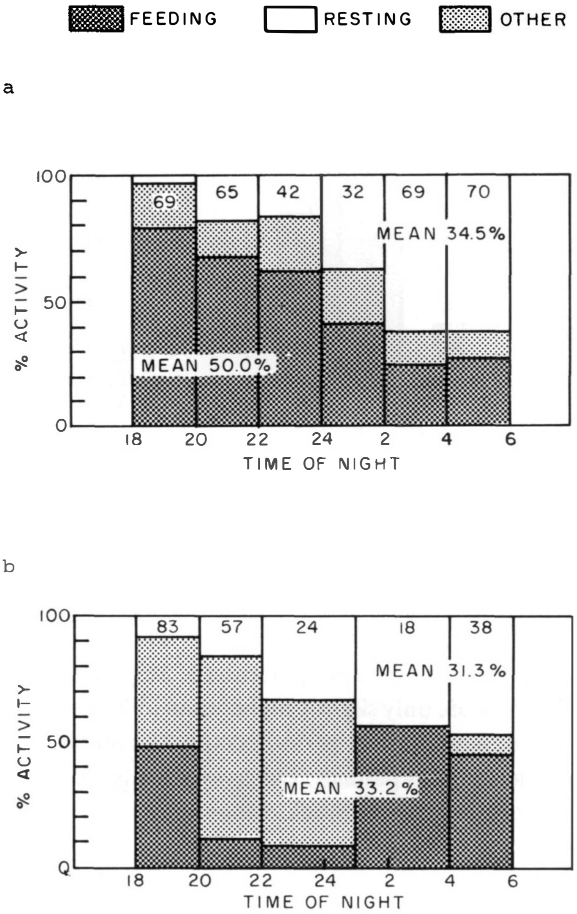


Fig. 4.2 Nocturnal activity pattern of white rhinos, for two times of the year. Figures indicate total sample sizes, in 15-min rhino activity units. a. *Wet season conditions* (data mostly March–June). b. *Dry season conditions* (data derived from June 1966 and July 1969, and biased towards neighborhood of waterholes).

main active periods were the early part of the morning, and the late afternoon, extending into the evening. A long rest was taken through the middle part of the day, during which period animals slept for up to eight hours under hot summer conditions. During the late summer period through January to March, the majority of rhinos were inactive between 09.00 and 16.00. The length of the inactive period was shorter during the cooler months of the early dry season of April–June, and if the weather was

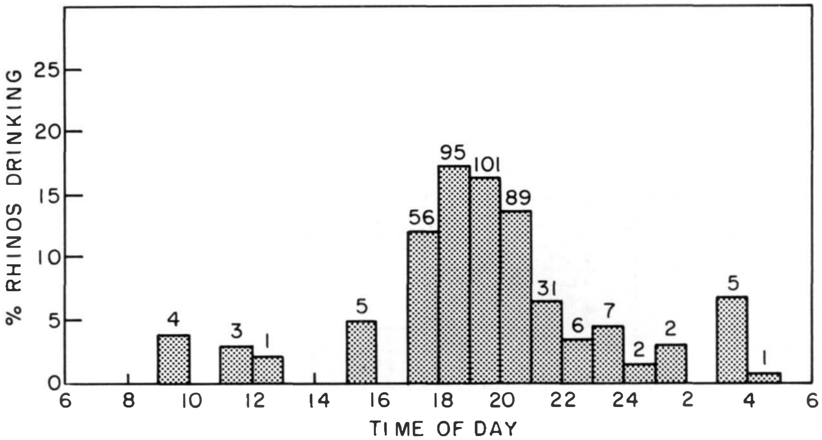


Fig.4.3 Drinking schedule of white rhinos at waterholes during the late dry season. Figures indicate total sample of rhinos observed drinking in each time interval (analyzed from composite records).

mild a feeding spell sometimes occurred over midday. Rhinos were less active over midday during the late dry season months of July–September, although mean temperatures were only slightly higher than those prevailing over the April–June period. Another rest period occurred through dawn, when animals commonly lay in sandy patches. The dawn rest disappeared in the late dry season. At this time of the year much of the evening was taken up by travelling to and from waterholes.

During the early wet season months of October–December, rhinos were more active during the day than they were during the later wet season, even though prevailing temperatures differed little between the two periods. Animals frequently interrupted their midday rest to revert to feeding for short spells, and much wallowing in pools or mud took place.

During cloudy weather rhinos were much more active during the day than they were under sunny conditions, with little seasonal variation. Short spells of feeding and resting alternated throughout the day, with relatively more time spent standing, neither feeding nor resting. On sunny days with a midday temperature of 24 °C the mean level of midday activity was 43%, compared with 81% on cloudy days with the same maximum temperature. Midday activity was depressed to 10% on sunny days with temperatures reaching 34 °C.

The main drinking period was in the early evening between 17.00 and 21.00 (Fig. 4.3).

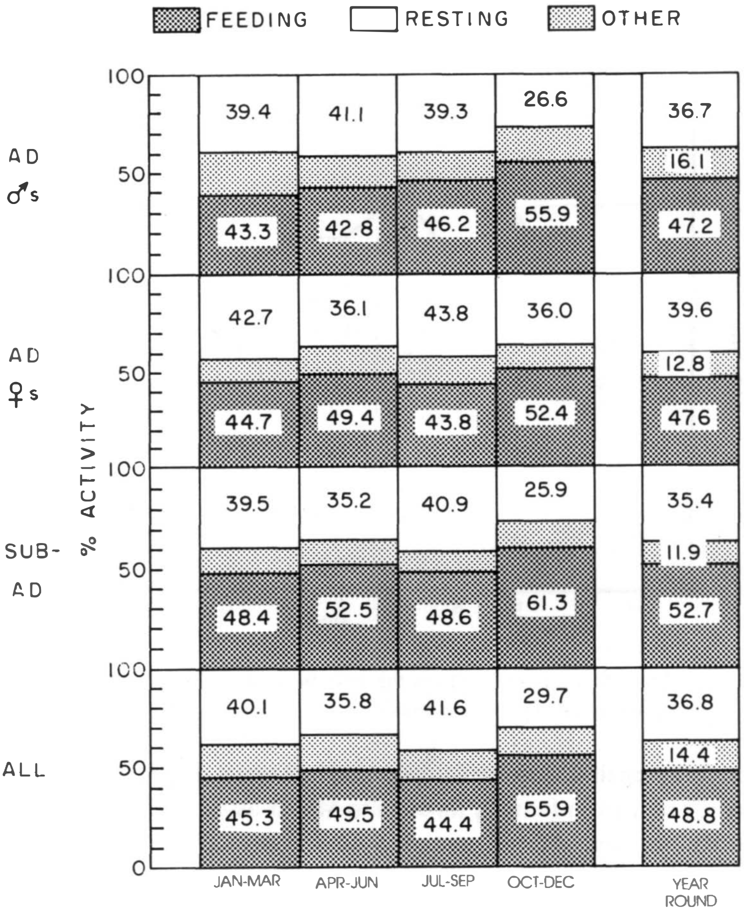


Fig. 4.4 Daytime activity budgets of white rhinos for different seasons and age/sex categories. Figures represent percentages.

As a year-round average for all age/sex classes, foraging occupied 49% of the daylight hours (Fig. 4.4) and about 50% of the night (Fig. 4.2). Adult males and adult females spent similar proportions of their time foraging over the year. However, females spent more time foraging than males during the early dry season, which followed the peak calving months of March and April. Cows that were either heavily pregnant or in early lactation spent more time foraging than other females at this time of the year. Subadults of both sexes devoted slightly more time to foraging than adults at all times of the year.

The daily foraging time for all age/sex classes peaked in November, while

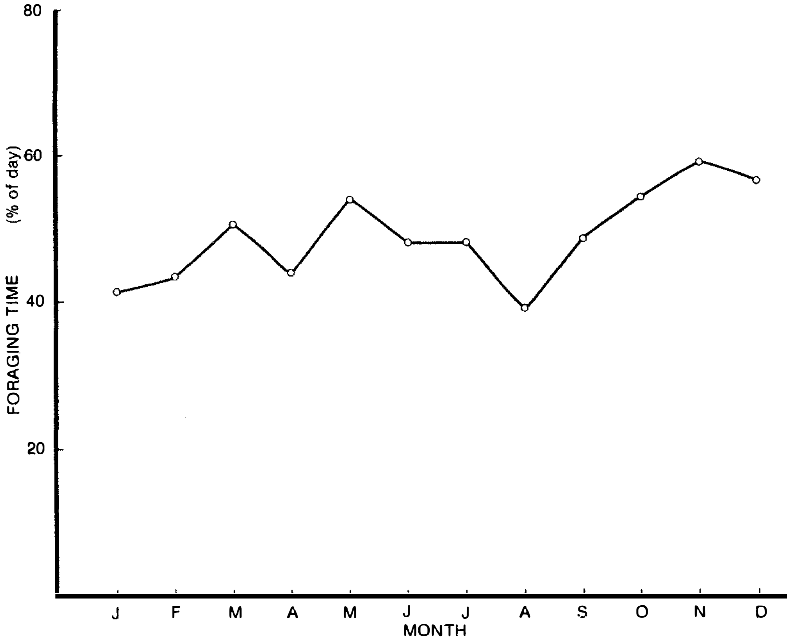


Fig. 4.5 Monthly variations in the daily foraging time of white rhinos (daytime only, all age/sex classes combined).

lowest foraging times were in January and in August (Fig 4.5). The increase in feeding time from January through to May is associated with decreasing mean temperature. After a minimum in August daily feeding time rose, despite rising temperatures after July.

Summary

Elephants of both species devote about three-quarters of their time to foraging, and spend relatively little time inactive. White rhinos, Indian rhinos, black rhinos and giraffes forage for 50–60% of the 24 hours; while for hippos foraging occupies no more than one third of the time. African elephants and white rhinos spend less time foraging in the dry season than in the wet season, whereas Indian rhinos and giraffes spend more time foraging in the dry season than in the wet season.

Giraffe are more active diurnally than nocturnally, and black rhinos more active nocturnally than during the day. Hippos accomplish all their feeding at night. Elephants, white rhinos and Indian rhinos are equally active during the day and night periods. However, all species except giraffe undertake most of their travelling, including journeys to and from water, shortly after nightfall.

Utilization of space

Animals tend to restrict their movements to a particular segment of the available habitat. The area traversed during routine activities is generally termed the home range (Jewell 1966); but what is routine is left vague. Walther (1972a) suggests that the home range is the area familiar to the animal, within which it establishes some space–time pattern of movement. However, there are occasions when animals wander beyond the limits of their usual home area. The term 'lifetime range' has been suggested for the total area covered by an animal, including temporarily used migration routes and exploratory sallies (Jewell 1966). However, unless observations are extended over a period comparable with the lifespan of the animal, the term 'annual range' seems preferable. This allows for the possibility that animals may move seasonally between different home ranges. Within the home range, certain sections may be used more frequently than others, these being referred to as 'core areas'. The term territory is applied only to areas that are defended, or at least monopolized by one particular individual or group to the exclusion of others.

Daily distances travelled may be measured along the path of movement, or simply as the straight-line distance between locations on successive days. The latter distance I will refer to as the 'daily translocation'.

Elephants

African elephants exhibit an exceptionally wide variability in home range extent. The home ranges of family units in the ground water forest habitat of Lake Manyara Park, Tanzania, covered only 14–52 km^2. In contrast, in the semi-arid steppe of Tsavo East National Park, Kenya, female elephants were radio-tracked over areas of up to 3750 km^2, with a mean of 1800 km^2. Under the wetter and topographically more diverse conditions of the adjoining Tsavo West Park, female ranges averaged 408 km^2 (based on two individuals). Male ranges had a mean extent of 1180 km^2 in Tsavo East and 840 km^2 in Tsavo West. The extensive movements in Tsavo East were monitored following a drought when much vegetation destruction and elephant mortality had occurred, and may thus have been exceptional. Preliminary data from the Kruger National Park in South Africa indicate range sizes of 240–720 km^2 for cows, and 140–1140 km^2 for bulls (Douglas-Hamilton 1972; Hall-Martin 1984; Leuthold 1977c).

Dry season home ranges cover only about 10% of the area of wet season ranges, and are based around permanent water sources. Distant areas are used opportunistically in response to local rainstorms and resultant green growth, areas having a dense grass cover being especially favored. Wet season dispersal movements away from permanent water were under 50 km in the Zambezi and Luangwa Valleys. However, movements over distances of 140 km or more between the Chobe and Hwange National Parks in Botswana and Zimbabwe respectively have recently been documented (G. Calef personal communication; Caughley & Goddard 1975; Dunham 1986; Leuthold 1977c; Melton 1985; Rodgers & Elder 1977).

Daily distances travelled average 4–6 km during daylight, and about 12 km over 24 hours. Walking speed is about 5–7 km h^{-1}. Mean daily translocation was 2.4 km at Manyara, 6 km at Tarangire and over 20 km at Serengeti (all in Tanzania), with wide day to day variability (Douglas-Hamilton 1971; Guy 1976b; Hendrichs 1971; Merz 1986b; Wyatt & Eltringham 1974).

For Asian elephants in the Ruhunu Park in Sri Lanka, home range sizes were estimated to be about 40 km^2, but surrounding settlements inhibited wider movements. Daily distances travelled during daylight varied between 1.0 and 8.5 km (McKay 1973).

Hippopotamus

Hippos in the Queen Elizabeth and Murchison Falls parks in Uganda had an area of heavy grazing extending up to 5 km from the lakeshore or river margin, with a mean extent of about 3 km. Some animals travelled as far as 10 km from water to graze at the end of the dry season. Along the Mara River in Kenya hippo paths generally extended 1.0–1.4 km from the river, with a maximum distance of 2.5 km. Along the Lundi River in Zimbabwe, the mean nightly distance travelled by hippos away from water varied from 0.4 km (maximum 1.2 km) during the wet season, to 0.7 km (maximum 2.1 km) during the dry season; but under drought conditions these distances increased to a maximum of 2.8 km in the wet season and 10 km in the dry season (Field 1970; Laws, Parker & Johnstone 1975; Lock 1972; Mackie 1973; O'Connor & Campbell 1986; Olivier & Laurie 1974).

Giraffe

Home ranges of female giraffe typically cover 80–120 km^2, but extended up to 480 km^2 in Tsavo East National Park. Seventy-five percent of sightings fell within a core area covering 30% of the total range. Home ranges of mature males tend to be slightly smaller than those of cows, while young adult males wander over a much wider area.

Daytime distances travelled averaged 6 km for males and 3 km for females in the Timbavati Reserve in South Africa; while daily translocation averaged 1.3 km (range 0.1–7.6 km) at Serengeti (Foster & Dagg 1972;

Langman 1973; Berry 1978; Leuthold & Leuthold 1978; Pellew 1981, 1984a).

Rhinoceroses

Indian rhinos at Chitwan occupied long narrow home ranges bordering the river. Individual cows were recorded over areas of up to 19.5 km², but most sightings fell within core areas covering 2–4 km². Male home ranges were similar in size (Laurie 1978, 1982). For Sumatran rhinos, home range extents of up to 50 km² were estimated, on the basis of the recognizable tracks of particular individuals (Borner 1979).

For black rhino cows home extent varied from a minimum of less than 2.6 km² in the Lerai Forest of the Ngorongoro Crater, Tanzania, to 99 km² on the Serengeti plains (Table 4.2). Typical home range sizes were about 7–35 km². However, desert-dwelling black rhinos in Namibia move over areas of up to 500 km². Home range sizes for adult males tended to be a little smaller than those of females, though the largest home range at Serengeti covered 133 km². Since these estimates include all sightings of particular animals, they represent annual ranges.

Animals moved over a wider area during the wet season than during the dry season, due to the availability of leguminous forbs in grassland areas at this time of the year (Goddard 1967; Hitchins 1971; Joubert & Eloff 1971; Loutit, Louw & Seely 1987; Mukinya 1973; Frame 1980).

White rhinoceros

I recorded the movements of white rhinos both by radio telemetry and by chance sightings of recognizable individuals. Six adult females, one young adult male, and three subadults were fitted with functioning radio transmitters. Transmitter life varied between 2.5 and 12.5 months. Methods are described elsewhere (Owen-Smith 1971b, 1974b).

The size of the area covered by white rhino cows varied depending on the prevailing habitat conditions. When both green grass and water were plentifully available, animals restricted their movements to a fairly small area, which may be termed the core area. During periods when the grass was drying out, movements were extended over a wider area. Such conditions were generally associated with the late wet season and early dry season months, but could occur temporarily during the wet season. The total area including such feeding movements will be termed the home range. Over the late dry season, when water sources became restricted to only a few points, movements further afield in the direction of one of the long-lasting water points were recorded. Between excursions to water, cows reappeared within

Table 4.2. *Home range extents of black rhinos in different areas*

Area	Age/sex	Range extent (km^2) Mean	Range extent (km^2) Min.–max.	Reference
Tanzania				
Ngorongoro	Adult female	15	2.6–26	1
	Adult female	16	2.6–44	
	Imm. female	28	14–58	
	Imm. male	36	14–58	
Olduvai	Adult female	36	3.6–91	
	Adult male	22	5.5–52	
	Imm. female	22	7.5–36	
	Imm. male	38	29–47	
Serengeti	Adult female	76	43–99	2
	Adult male	92	59–133	
Kenya				
Mara	Adult female	14	5.6–23	3
	Adult male	13	7.1–19	
South Africa				
Hluhluwe	Adult female	6.7	5.8–7.7	4
	Adult male	4.1	3.7–4.7	
Umfolozi	Adult female	10	—	5

Note: Imm. = Immature.
Source references: 1 – Goddard 1967; 2 – Frame 1980; 3 – Mukinya 1973; 4 – Hitchins 1971; 5 – personal observations.

their usual home ranges. Animals with a permanent water point within their home range did not exhibit these excursions. Thus the water corridors are regarded as temporary additions to the home range (Fig. 4.6). Home ranges of cows covered between 9 and 15 km^2. Core areas encompassed 5–10 km^2, and annual ranges including water corridors covered an area of 8.9–20.5 km^2 (Table 4.3). Some cows moved beyond radio-tracking range, so that the latter figures must be regarded as a minimum estimate of the annual range.

Home ranges of adult males covered 0.7–2.6 km^2; but since these were mutually exclusive, they represent territories and will be discussed in Chapter 7 under social organization.

Though defined on the basis of habitat conditions, the core areas were the most favored sections of the home ranges of cows at all times of the year. For the two best-known cows, 72% of all points of location over the year fell within the core area. Movements beyond the core area seemed to represent random probes in search of better grazing conditions. Drying conditions

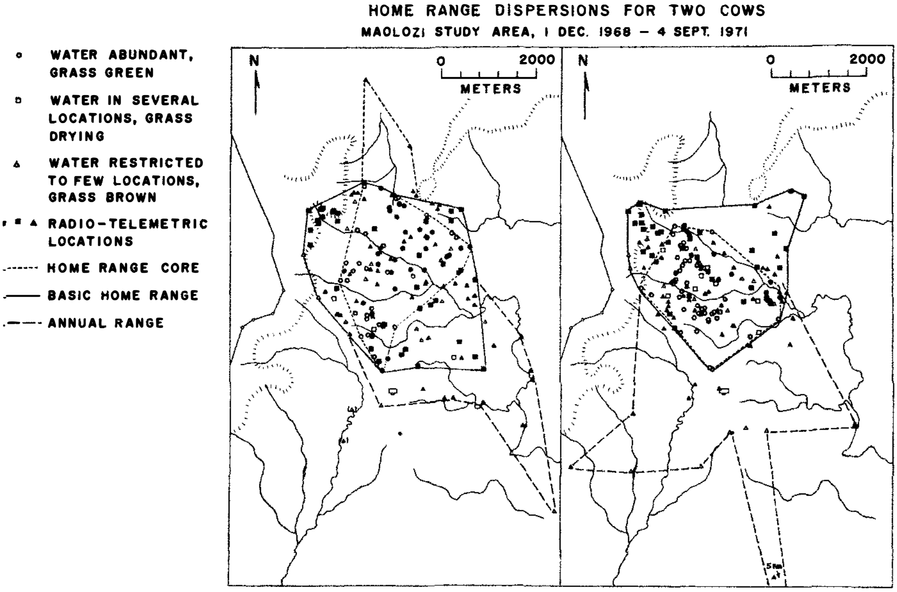


Fig. 4.6 Home ranges of two white rhino cows at Umfolozi, showing delineation of the core area and the dry season extensions in relation to grass condition and water availability. From Owen-Smith 1975.

prompted a general shuffling around of individuals, as also did the arrival of rains breaking a dry spell. When grass was green and water plentiful, cows remained grazing in the same area of about 1–2 km^2 for several consecutive days.

The observed distance covered by white rhinos during a 24 hour period was 4–5 km under wet season conditions. Daily translocation distances varied little through the year, apart from journeys to and from water in the late dry season (Table 4.4). Some cows travelled routinely a distance of 6–8 km to a waterhole and back every 3–4 days towards the end of the dry season. The furthest distance that a white rhino bull had to travel from his territory to water and back was nearly 10 km, involving a total time of 4–5 hours out of his territory on each occasion. Longer journeys were necessary after waterholes away from the two Umfolozi rivers had dried up. One cow moved overnight a distance of 11 km to the Black Umfolozi River, but was back in her usual home range a day later following a thunderstorm which broke the winter drought. The walking speed of white rhinos travelling to water was about 3 km h^{-1}.

Occasional wandering movements over greater distances may be made. One cow with a distinctive horn shape that occasionally visited my study

Table 4.3. *Home range sizes of white rhinos at Umfolozi*

Areas measured planimetrically after connecting outlying points. Upper figure represents the mean area, lower figures (in brackets) the range in area.

Age/sex class	No. of individuals	Area (km²)		
		Core area	Home range	Annual range
Adult female	8	6.7 (5.3–9.6)	11.6 (8.9–14.7)	16.2 (8.9–20.5)
Adult male	27	1.7 (0.8–2.6)	—	—
Imm. female	2	5.0 —	6.0 (5.0–7.0)	7.3 —
Imm. male	4	4.6 (4.3–5.0)	4.6 (2.2–7.0)	6.7 (6.1–7.3)

Note: Imm. = Immature.

Table 4.4. *Daily translocations by white rhino cows*

Based on straight-line distances between early morning locations on successsive days.

Conditions	Translocation distance (km)		*N*
	Mean	Min.–max.	(days)
Late wet season	1.20	0.1–2.3	12
Early dry season	1.47	0.05–3.1	16
Late dry season	1.66	0.2–5.1	25
	1.16[a]	0.2–2.8[a]	18
End of dry season	1.69	0.15–4.0	37

Note: [a] Excluding waterhole movements.

area was seen by a park ranger 13 km away. Another cow with a broken off anterior horn was seen grazing the green flush following a fire on the hillslopes to the west of my study area in November, 1968, when conditions were generally very dry. She was not seen again in the study area, but a broken-horned cow, which was almost certainly the same individual, was seen from the road some 28 km to the east.

Some subadult white rhinos appeared resident in the study area, while others wandered in, remained for a period, then disappeared again. Home range extents of resident subadults varied between 2.1 km² and 7.3 km². Two subadult females marked with eartags in the study area were subsequently seen 15 km and 25 km away respectively. Thus a proportion of subadults had evidently not established a fixed home range.

In the Kyle Game Park in Zimbabwe, white rhino cows were recorded moving over home ranges of up to 20 km^2. In the Murchison Falls National Park in Uganda, female white rhinos of the northern race (which had been moved there from west of the Nile River) covered annual ranges of between 50 km^2 and 97 km^2. Similarly large home ranges have been observed for animals of the southern race introduced into the Kruger Park in South Africa (Condy 1973; A. J. Hall-Martin personal communication; van Gyseghem 1984).

Summary

African elephants move over large annual ranges typically covering several hundred square kilometres, while giraffe also move over large areas a hundred or more square kilometers in extent. Rhinos of various species occupy somewhat more moderate-sized ranges typically covering 10–100 km^2, excluding movements to water. Asian elephants occupy restricted home ranges in sanctuaries, but may have moved over somewhat larger areas in the past.

African elephants move seasonally between a restricted dry season range near permanent water, and a wet season expansion area, which they use opportunistically in response to rainfall and resultant vegetation growth. A similar pulsating pattern is shown by black rhinos, at least in relatively open grassland habitats, and giraffe. In contrast, white rhinos restrict their movements during the wet season, and move over a larger feeding area during the dry season.

Comparisons with smaller ungulates

Medium-sized ungulates typically devote 35–60% of the daytime to foraging (Duncan 1975; Jarman & Jarman 1973a; Owen–Smith 1979; Stanley-Price 1977; Spinage 1968). This is not very different from the proportion of the daylight hours spent foraging by megaherbivores (50–75%, except for hippos). However, megaherbivores (excluding giraffe) are equally active, or even more active, at night as during daylight; while medium-sized ungulates (from gazelle size upwards) spend less time feeding and more time ruminating at night than in the daytime. Thus over a 24 hour cycle smaller ungulates feed for less time than do megaherbivores, excepting hippos.

Many grazing ungulates show decreased feeding times during the late dry season. White rhinos and African elephants do likewise. This effect may be largely due to the constraint on digestive throughput rates imposed by the slow digesting forage such as dry grass or woody twigs and bark. However, another factor to be considered, at least in the case of white rhinos, is the increased height of the grass eaten during the dry season compared with the wet season, so that more herbage is ingested per bite. Notably white rhinos spent the greatest proportion of their time feeding during the early wet season when the grass was shortest.

While the ranges covered by African elephants are large, they are exceeded in extent by the area covered by migratory antelope such as the Serengeti wildebeest, which may encompass up to 20 000 km^2 annually (Pennycuick 1975). Migratory zebra move over ranges covering several hundred square kilometers (Klingel 1967). Other wide-ranging species of bovid move over home ranges equal or larger in size to those covered by rhinos and giraffe, for example African buffalo (Leuthold 1972; Sinclair 1977) and both roan and sable antelope (Joubert 1974; Estes & Estes 1974).

5

Body size and nutritional physiology

Introduction

An animal's food choice is constrained by its metabolic requirements and by the functional anatomy and physiology of its digestive tract. In this chapter I consider how these constraints operate, and how their effects vary with body size. For example, larger animals generally eat more food per day than smaller animals. However the more critical sorts of questions that I will ask are these:

1. Does a 5000 kg elephant bull eat 1000 times as much food per day as a 5 kg dikdik?
2. What allometric relation best predicts the trend in food intake with increasing body mass?
3. Do particular species deviate notably from the overall trend, in particular those of very large body size?

In this chapter and others of its kind I will introduce each section with a deductive proposition as to how the particular attribute being considered ought to vary in relation to body mass. I will then test whether the published data on large herbivores support or refute this starting hypothesis. The statistical technique to be used is that of least squares regression. The reader must first be forewarned of potential pitfalls in this method, as discussed by Peters (1983).

1. Standard regression techniques assume that the X-variate (i.e. body mass in our case) is measured without statistical error. Generally I will use the mean body mass for the age/sex category being considered (see Appendix I), except in those few cases where more precise figures are available for the particular animals observed. Some error may be introduced here, but it should be fairly minor on a log scale.
2. The major influence on the slope of the regression line is exerted by the extreme points; in our case the values reported for very small

and very large animals. To allow for a possible biasing influence by megaherbivores, I will report regression coefficients for the subset of data excluding megaherbivores as well as for the complete set.

3. Values for the coefficient of determination R^2 are influenced by the total range of variation in the data, since this parameter represents the reduction in variance accounted for by the regression line. Thus, data for a sample of animals varying widely in body size will tend to yield a higher value for R^2 than any subset of the same data spanning a narrower range in body mass.

Potential biological pitfalls in using published data for comparative purposes were discussed by Clutton-Brock & Harvey (1977a):

1. Reported differences between species could be due to differences in the methods used in the particular studies. I have alluded to some of these in the preceding chapters, e.g. the distinction between foraging time and feeding time, and between annual and seasonal ranges.
2. The available data may be unrepresentative of particular species, especially where ecological features vary seasonally or between different regional populations or habitat types. Wide intraspecific variability in home range sizes was clearly evident in Chapter 4 both for African elephant and black rhino. For most ungulates, quantitative data are restricted to a single, supposedly definitive, study.
3. The data may be weighted heavily towards particular taxonomic groups, and thus not be typical of large herbivores in general. However, as will be evident in the graphical plots that follow, published studies now span a wide range of ungulate species. Thus, for most ecological features biases of this kind should be less than what they might have been one or two decades ago.

Nevertheless, the empirically derived relationships presented should be regarded as suggestive rather than as conclusive, awaiting more critical testing by matched comparisons or directed experiments.

Metabolic requirements

The basal or maintenance energy requirements of a wide range of animals, measured in calories or joules per day, vary in relation to $M^{0.75}$, where M represents body mass (Kleiber 1961; Peters 1983; Schmidt-Nielsen 1984). Linstedt & Calder (1981) suggest that this follows from underlying physiological mechanisms. The time periods for a wide range of processes, from muscle twitch times to potential lifespans, vary as a function of body mass raised to the power about one quarter. Hence metabolic rate, which represents a volume factor (the animal's size) divided by a time factor, is scaled in relation to $M^{1.0}/M^{0.25} = M^{0.75}$. By similar basic algebra, the specific metabolic rate per unit of body mass decreases with body size in relation to $M^{-0.25}$ (i.e. $M^{0.75}/M^{1.0}$). The factor $M^{0.75}$ is referred to as the metabolic mass equivalent. In terms of this relation, the maintenance energy requirements of a 5000 kg elephant should be only 180 times those of a 5 kg dikdik, rather than a thousand times as great.

The above relations refer strictly to maintenance requirements, with no allowance made for the extra costs for activity or growth or for temperature regulation. Daily metabolic expenditures measured for 23 species of eutherian mammals under natural conditions (using doubly-labelled water) varied according to a scaling coefficient of 0.81. However, three of the four large mammal species for which data were available were pinnipeds, which tend to exhibit higher metabolic rates than other mammals. For herbivores alone, field metabolic rate scaled in relation to $M^{0.73}$, although the only large herbivore included was white-tailed deer (Nagy 1987). In the absence of further information, I will provisionally assume that the daily metabolic requirements of large herbivores vary similarly according to a scaling coefficient of 0.73.

Protein requirements are derived from two components: (i) endogenous urinary nitrogen excretion, which is related to protein turnover and hence to metabolic rate; (ii) fecal nitrogen losses, including not only undigested protein but also enzymes added during digestion and cells sloughed off from the digestive tract lining. Fecal nitrogen losses are related to the quantity of food processed rather than directly to metabolic rate. Protein requirements vary even more widely than energy needs in relation to growth increments and reproduction.

Gut anatomy

As a volume factor, the capacity of the digestive tract should increase in direct proportion to body mass, in the absence of any adaptive trends. Despite contrasting digestive anatomies, the capacity of the fermentation chamber (as measured by the wet mass of its contents) forms a similar fraction of body mass in both foregut and hindgut fermenters, as also does the total digestive capacity of the gastro-intestinal tract. However the mass of gut contents increases in relation to $M^{1.08}$, rather than $M^{1.0}$ (Paraa 1978).

Demment (1982) compared the ruminoreticulum capacity of a variety of African ungulates, as measured by liquid filling, against the capacity as indicated by mass of contents. He found that, while the mass of ruminoreticulum contents increased in relation to $M^{1.11}$, liquid fill capacity varied in relation to $M^{0.94}$. It is likely that contents mass underestimates the ruminoreticulum capacity of small ungulates, because their rumens are often not filled to capacity; while liquid fill overestimates capacity for small species, with rumen walls that are thinner and thus more prone to stretching. The best estimate for the power coefficient of variation between gut capacity and body mass is hence the mean of the above two estimates, i.e. 1.03. Thus overall gut capacity, as well as the capacity of the fermentation chambers (whether ruminoreticulum or cecum plus colon), effectively increases in direct proportion to body size.

Food intake and digestion

Jarman (1968, 1974) and Bell (1969, 1971) focussed attention on patterns of food selection among African ungulates of varying body size. They noted that, while specific metabolic rate decreases with increasing body mass, gut capacity remains a constant fraction of body mass. Hence larger ungulates should be able to tolerate a lower minimum dietary quality than smaller species. Geist (1974a) labelled this concept the 'Jarman–Bell Principle'.

Bell (1971) noted further that the turnover rate of rumen contents decreases with increasing fiber content of the diet, due to the fact that particles have to reach a certain degree of comminution before they can pass out of the ruminoreticulum through the narrow passage connecting it to the rest of the gut. This restriction does not apply to non-ruminants like zebras, which hence show a faster passage rate of material through the gut than ruminants. Thus a non-ruminant should be able to tolerate a diet of higher fiber content, and thus lower nutritional quality, than a ruminant of similar body size (see also Janis 1976).

More specifically, if nutrient requirements increase in proportion to metabolic expenditures, and food intake is restricted directly by gut capacity, nutrient concentrations in the diet should vary as a function of $M^{-0.30}$ ($M^{0.73}/M^{1.03}$). This means that if a 5 kg dikdik required a diet that was 80% digestible, a 5000 kg elephant would be able to accept a diet that was only 10% digestible. However, this assumes that: (i) the turnover rate of the digestive tract contents remains constant; and (ii) digestive efficiency is the same. In fact, more nutritious herbage ferments faster than more fibrous material, and hence passes through the digestive tract more rapidly. Digestive efficiency is influenced by passage rate. Material that passes through the fermentation chamber faster is fermentated less completely than material that is retained for longer. Thus non-ruminants like horses show a lower digestive efficiency, in terms of cell wall breakdown, than ruminants.

In compensation the more rapid rate of food passage allows non-ruminants to eat more food per day than ruminants. On high fiber diets non-ruminants may assimilate more nutrients per unit time than ruminants, despite the superiority of the latter in extent of digestion.

Demment & Van Soest (1985) noted that: (i) the retention time of digesta in the gut tends to get longer as absolute gut capacity increases with increasing body mass, and (ii) the extent of digestion of cell wall is a function of retention time. Hence they suggest that at some body mass hindgut fermenters should be able to achieve virtually complete digestion of potentially digestible cell wall components, despite the absence of the selective delaying structures promoting efficient digestion in the rumen of ruminants. From model calculations, they suggest that this should happen at a body mass of 600 kg for rapidly fermenting forage (such as dicotyledonous foliage), or 1200 kg for slowly fermenting forage (such as grass leaves). Interestingly, these values lie close to the size criterion for megaherbivores adopted in this book.

Foose (1982) investigated the comparative digestive efficiencies of foregut and hindgut fermenters. The 36 species of large herbivore that he studied span a wide range in body size, so that his data also reveal the effects of body mass on digestive processes.

Foose's measurements were carried out on captive animals held in zoos, and are thus subject to the limitations that these conditions impose, not least of which is the limited sample of animals of each species that could be studied. Two fairly standardized diets were fed: (i) a high fiber grass hay, varying between 4.5% and 7.4% crude protein and 65–70% cell wall content (assayed as neutral detergent fiber); (ii) a moderate fiber content legume (alfalfa) hay, containing 17.4–22.2% crude protein and 31–56% cell wall constituents. The measures that we are interested in are (i) rate of food intake, (ii) rate of digestive passage, (iii) efficiency of cell wall digestion and (iv) overall nutritional balance.

Daily food intake

Foose's data show a decline in organic matter intake, expressed as a proportion of body mass, with increasing body mass (Fig. 5.1). For the grass hay the correlation is only marginally significant, and is due only to the equids, which as a group exhibit food intakes per unit of body mass about twice those of other ungulates of comparable body mass. For the legume hay, on the other hand, the correlation is highly significant. (Giraffe and pigmy hippos, which were reluctant to eat the hay diets, have been omitted from the regressions).

Evidently the food intake of foregut fermenters is restricted on the low

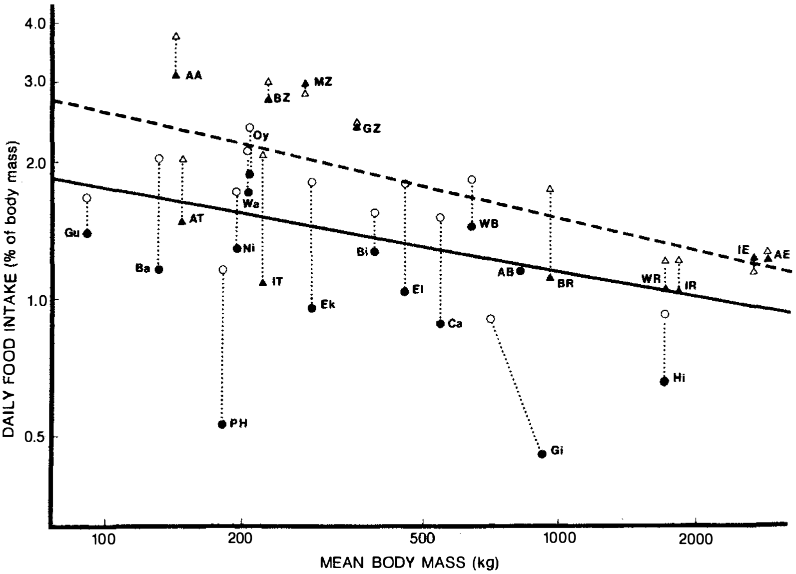


Fig. 5.1 Daily food intake, expressed as organic matter, in relation to body mass, from the work of Foose (1982) using standardized diets. Solid = grass hay, open = legume hay, circles = foregut fermenters, triangles = hindgut fermenters. For key to species labels, see Appendix I.
Regressions:
(i) grass hay, all species except pigmy hippo and giraffe (solid line): Daily Food Intake (*DFI*) (organic matter as % of body mass) = $4.04M^{-0.184}$ (SE(b) = 0.074, $R^2 = 0.217$, $N = 24$, $P < 0.05$).
(ii) grass hay, hindgut fermenters only: $DFI = 6.95M^{-0.236}$ (SE(b) = 0.101, $R^2 = 0.376$, $N = 11$, $P = <0.05$).
(iii) legume hay, all species except pigmy hippo and giraffe (dashed line): $DFI = 7.31M^{-0.231}$ (SE(b) = 0.049, $R^2 = 0.500$, $N = 24$, $P < 0.0001$).
(iv) legume hay, hindgut fermenters only: $DFI = 13.8M^{-0.315}$ (SE(b) = 0.049, $R^2 = 0.819$, $N = 11$, $P < 0.001$).

quality grass hay, but not with the faster digesting legume hay. For hindgut fermenters on the legume hay diet, the slope of the regression (0.31) is almost identical to the value needed to compensate for metabolic rate variations (0.30). Equids in particular compensated for their higher specific metabolic rates relative to larger hindgut fermenters by means of increased food intakes. However, this does not represent a facultative increase in intake to compensate for poor digestibility (as implied by Janis 1976), but is rather a constitutive anatomic ability to process more food per day than similar sized ruminants. In Foose's experiments the equids generally ate less of the grass hay than of the legume hay, indicating that their food intake was

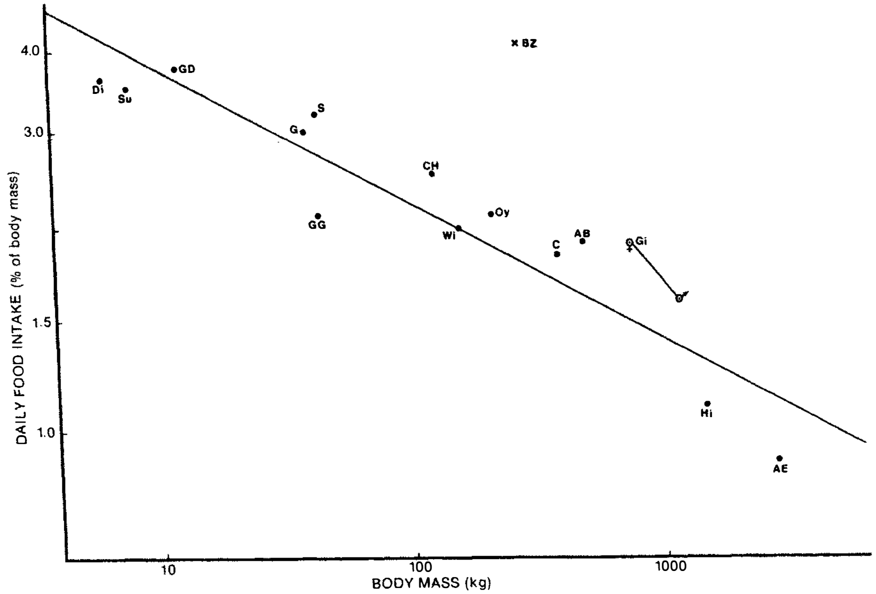


Fig. 5.2 Daily food intake in relation to body mass, from various published sources. For key to species labels, see Appendix I. Data from Arman & Field (1973), Arman & Hopcraft (1975), Hoppe (1977a), Laws *et al.* (1975), Nge'the (1976), Pellew (1984c), Sinclair (1977) and Taylor & Maloiy (1967). Regression: Daily Food Intake (dry mass as % of livemass) = $6.0M^{-0.191}$ (SE(b) = 0.039, $R^2 = 0.647$, $N = 15$, $P < 0.01$).

constrained on poor quality forage, but to a much lesser degree than was the case for ruminants (see also Hintz *et al.* 1978).

Other data reported in the literature using various diets show a significant tendency for food intake per unit of body mass to decrease with increasing body mass (Fig. 5.2). In particular, the daily food intake of the smallest antelope represents 3.5–4.0% of body mass, compared with only about 1% of body mass for hippos and elephants. For cattle and other medium sized ruminants, daily food intake ranges between 1.5% and 3.0% of body mass. The majority of the available data refer again to captive animals fed standardized rations, except in the case of megaherbivores (see Chapter 3).

Thus large herbivores do tend to eat less food per day, as a proportion of their body mass, than small herbivores. For hindgut fermenters fed standardized diets, the decline in mass-specific food intake with increasing body mass parallels the corresponding decrease in metabolic requirements; while for ruminants the compensation is only partial, particularly for the low quality grass forage. The mass-specific food intakes of megaherbivores are

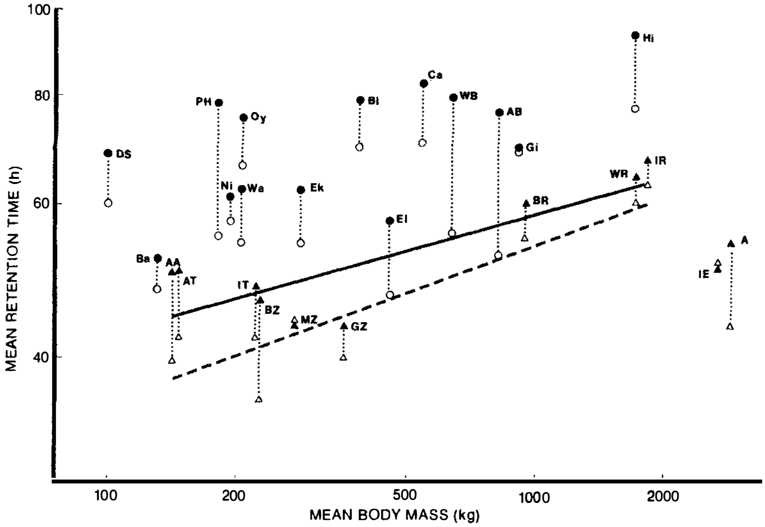


Fig. 5.3 Mean retention time of digesta in relation to body mass, from the work of Foose (1982) using standardized diets. Solid = grass hay, open = legume hay, circles = foregut fermenters, triangles = hindgut fermenters. For key to species labels, see Appendix I.

Regressions:

(i) grass hay, all species: Retention Time RT (in hours) = $46.1M^{0.048}$ (SE(b) = 0.044, $R^2 = 0.046$, $N = 26$, P not significant).

(ii) grass hay, hindgut fermenters only: $RT = 32.0M^{0.075}$ (SE(b) = 0.033, $R^2 = 0.358$, $N = 11$, $P < 0.05$).

(iii) grass hay, perissodactyls only (solid line): $RT = 22.8M^{0.135}$ (SE(b) = 0.035, $R^2 = 0.673$, $N = 9$, $P < 0.01$).

(iv) legume hay, all species: $RT = 36.6M^{0.061}$ (SE(b) = 0.040, $R^2 = 0.088$, $N = 26$, P not significant).

(v) legume hay, hindgut fermenters only: $RT = 23.4M^{0.106}$ (SE(b) = 0.035, $R^2 = 0.504$, $N = 11$, $P < 0.05$).

(vi) legume hay, perissodactyls only (dashed line): $RT = 12.8M^{0.177}$ (SE(b) = 0.28, $R^2 = 0.849$, $N = 9$, $P < 0.01$).

typically about half those of medium-sized ruminants and about one quarter those of equids.

Retention time

In Foose's experiments the rates of digestive passage were assessed by mixing a proportion of dye-marked hay with the forage and recording the time of appearance of increasing fractions of the dye in the feces. From these data the mean retention times of food residues in the gut (the inverse of passage rates) were calculated.

In the overall data set, combining both foregut fermenters and hindgut

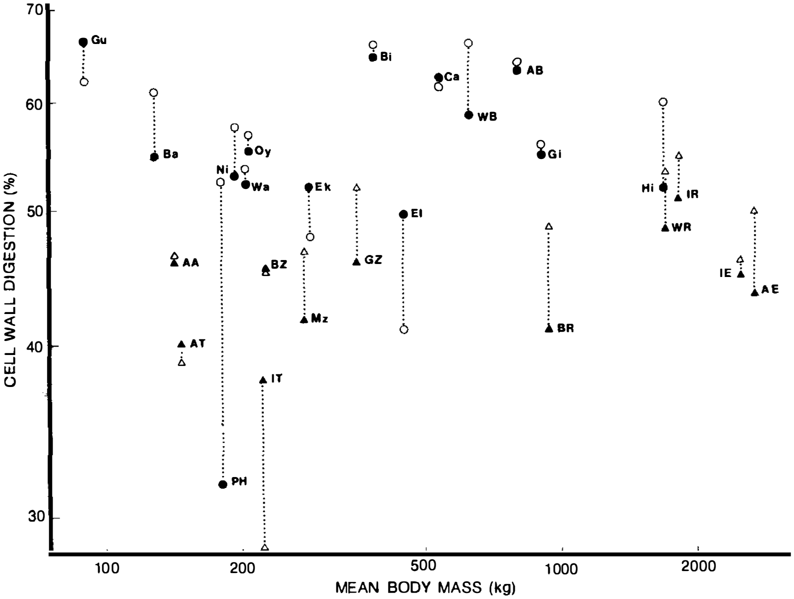


Fig. 5.4 The extent of cell wall digestion achieved in relation to body mass, from the work of Foose (1982) using standardized diets. Sold = grass hay, open = legume hay, circles = foregut fermenters, triangles = hindgut fermenters. For key to species labels, see Appendix I.

fermenters, there is no correlation between mean retention time and body mass (Fig. 5.3). However, for perissodactyls retention times do show a significant tendency to increase from tapirs and equids through to rhinos. Moreover, hindgut fermenters show shorter retention times (or faster passage rates) than foregut fermenters of similar body mass. Elephants exhibit retention times intermediate between those of equids and rhinos; while hippos exhibit an exceptionally long retention time, amounting to almost four days for the grass hay diet. The retention times shown by the two largest rhino species are comparable with those of some of the medium sized ruminants, such as waterbuck and American elk, though not as great as those of bovines or camels.

Digestive efficiency

The extent of digestion of grass cell wall achieved by the two grazing rhinos was somewhat less than that shown by grazing ruminants (Fig. 5.4) (apart from eland, a species which despite its mixed diet has the rumen anatomy typical of a browser; Hofmann 1973). Hippos, despite a long retention time, achieved a cell wall digestion only marginally greater

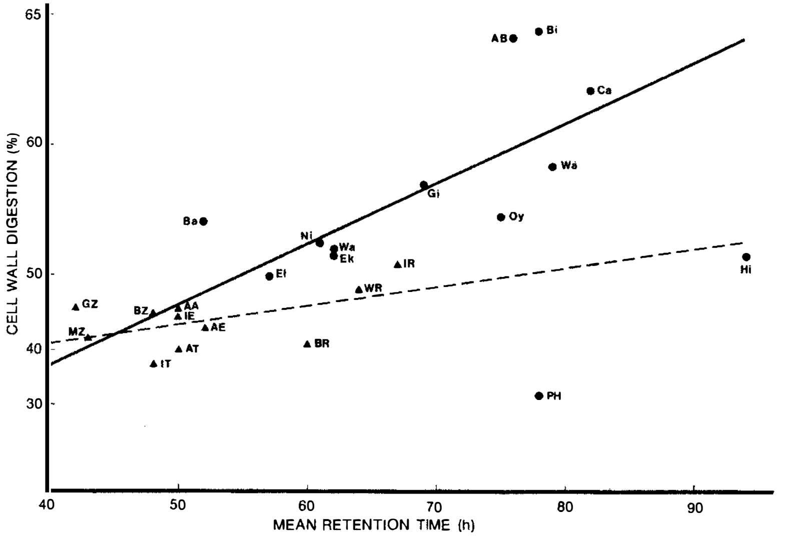


Fig. 5.5 The extent of cell wall digestion achieved in relation to mean retention time for grass hay diets, from the work of Foose (1982). The Y-axis has been scaled in terms of the log of the residual amount of digestible cell wall remaining, based on Waldo *et al.* (1972). It is assumed that the potential cell wall digestibility is 70%.
Regressions:

(i) all species, except for hippos: Log_e (residual digestible cell wall *RDCW*, as %) = 4.95 − 0.034 (mean Retention Time *RT*, in hours) ($R^2 = 0.721$, $N = 23$, $P < 0.001$).

(ii) foregut fermenters, excluding hippos (solid line): Log_e (*RDCW*) = 4.75 − 0.032 *RT* ($R^2 = 0.588$, $N = 12$, $P = < 0.05$).

(iii) hindgut fermenters (dashed line): Log_e (*RDCW*) = 3.77 − 0.010 *RT* ($R^2 = 0.292$, $N = 11$, P not significant).

than that of the grazing rhinos. However, the two largest rhinos attained a higher cell wall digestion than equids despite their similar digestive anatomy, and also digested the grass hay somewhat better than did the elephants despite the body size advantage of the latter.

However, to compare digestive efficiencies among different categories of herbivore, the effects of varying retention time need to be separated out. For domestic ruminants, the rate of cell wall digestion has been found to follow linear kinetics, if the indigestible fraction is subtracted from the total cell wall pool (Waldo *et al.* 1972). This means that the log of the residual amount of digestible cell wall remaining should be linearly related to time. Thus a plot of this function against time reveals differences between species in their rates of cell wall digestion.

The measurements made by Foose (1982) indicate that hindgut fermenters achieve a lower extent of cell wall digestion than ruminants for the same retention time (Fig. 5.5). Moreover, the extent of cell wall digestion increases more rapidly with time in ruminants than among hindgut fermenters. At the short retention times typical of equids the two regression lines cross, suggesting that there is not much difference in cell wall digestion between foregut fermenters and hindgut fermenters for retention times of the order of two days. Elephants appear no different from equids in their rate efficiency of digestion. Hippos exhibit a rate efficiency of cell wall digestion that fits the regression line derived for hindgut fermenters, with pigmy hippos notably inefficient.

Nutritional balance

It was hypothesized by Bell (1971), Janis (1976) and Foose (1982) that nonruminants should outperform ruminants on forages of high fiber content, since their food passage rate is not slowed down much by indigestible material. Furthermore, on account of their very large body size and hence low specific metabolic rate, elephants and rhinos should be the most successful among extant species at utilizing low quality forage.

Foose (1982) estimated rates of energy extraction from the extent of digestion of the organic matter content of the diets supplied, and standardized values for the energy content of plant tissues. Energy gains were then related to energy requirements, estimated to be about 1.5 times basal metabolic rate calculated on the basis of $M^{0.75}$. His results indicate that equids, rather than rhinos or elephants, were best able to extract energy from the low quality grass hays (Fig. 5.6). However, elephants and rhinos were as successful as most of the bovids; while hippos, despite their large body size, were unable to meet their energy requirements from the grass hay diet. Giraffes and pigmy hippos were notably unsuccessful on both diets. Black rhinos performed poorly on the grass diet, but did very much better on the legume hay, due largely to the much higher rates of food intake that they showed for the latter.

Foose (1982) made similar calculations for protein balance. This appeared to be less restrictive than energy balance, although no allowance was made for protein needed during pregnancy and lactation. However, the nutritional value of the temperate grass hays used in Foose's experiments was considerably higher than that typical of tropical (C_4) grass species during the African dry season (see Owen-Smith 1982). Thus Foose was unable to identify the lowest tolerance limits in terms of dietary quality for the large herbivore species that he investigated.

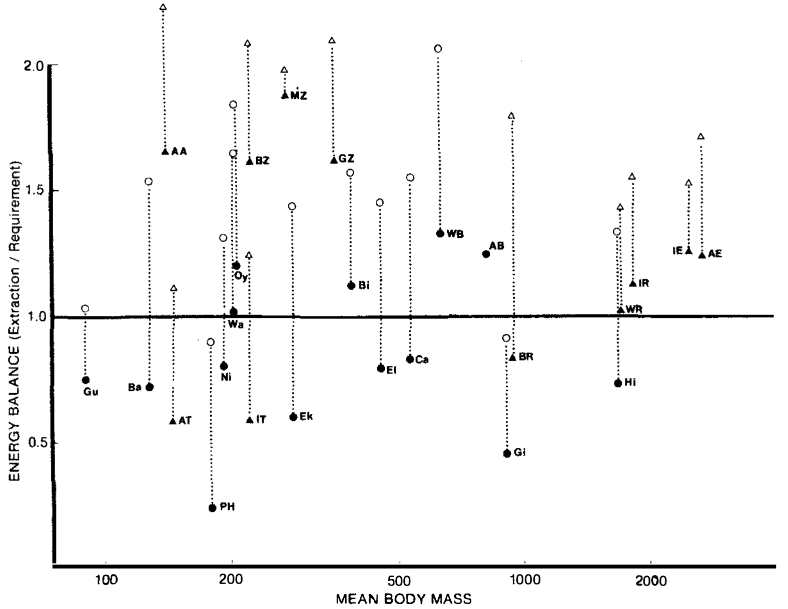


Fig. 5.6 Nutritional balance for energy calculated from Foose's (1982) measurements, for standardized diets. Solid = grass hay, open = legume hay, circles = foregut fermenters, triangles = hindgut fermenters. For key to species labels, see Appendix I.

Summary

In summary, different megaherbivores employ varying strategies to cope with low quality forage:

1. Elephants show a moderate food intake and fairly rapid turnover rate of digesta relative to their body mass. Because of their large size they achieve similar digestive efficiencies to equids, but with a lower specific food intake. Notably, both surviving species of elephant are mixed feeders, adapted anatomically (at least in their dentition) to handle both grass and woody browse.
2. Rhinos gain an advantage from their large body size relative to other perissodactyls in the form of increased retention times. This allows them to achieve a greater extent of cell wall digestion than equids and tapirs, though less complete than that attained by medium-sized ruminants. The black rhino, a browser, appears to be less efficient at cell wall digestion than the two grazing rhino species, though this may be partly a consequence of its smaller body size.

3. Hippos rely on an extremely long retention time to eventually achieve fairly complete digestion of cell wall components, but at the expense of a restricted rate of food intake. Foose (1982) suggested that, due to their semi-aquatic habits and consequently low thermoregulatory demands, hippos may have a lower metabolic requirement per unit of body mass than other ungulates.
4. Giraffe performed poorly on the diets supplied, due either to their difficulties in ingesting the forage supplied, or to an inability to digest the high fiber content

6

Body size and feeding ecology

Introduction

It is evident from Chapters 3 and 4 that megaherbivores select high quality green herbage or fruit when these are available, but switch to more fibrous forage during the dry season when choice is restricted. In superficial terms this pattern is not very different from those displayed by smaller ungulates, except for the amount of woody material eaten by elephants at times. Megaherbivores tend to forage for longer over the 24 hour day than do smaller ruminants; but daily foraging times are similar to those of medium-sized non-ruminants like zebras. The home range sizes of megaherbivores are no larger than those of many medium-sized ungulates, again with elephants being a clear exception. To discern body size influences, quantitative data for a range of species of widely varying body size need to be examined.

Diet quality

The nutritional value of food ingested must be adequate to satisfy metabolic demands, otherwise survival chances will be reduced. From the results reported in Chapter 5, total daily metabolic requirements (for maintenance plus activity) are predicted to vary with body size as a function of $M^{0.73}$. The assimilation rate of nutrients depends both on the capacity of the digestive tract and on the passage rate of its contents. Larger animals can support their lower specific metabolic requirements either by eating less food per day, or by accepting food with lower nutrient concentrations, or some combination of both. The data reported in Chapter 5, based largely on captive animals, suggest that daily food intake declines with increasing body mass approximately in relation to $M^{-0.2}$ (Figs. 5.1 and 5.2), while gut capacity is proportional to $M^{1.03}$. This implies that diet quality should vary as a function of $M^{-0.10}$ $\{(M^{0.73}/M^{1.03})/M^{-0.2}\}$. In other words, larger animals should eat diets of lower nutritional value than those selected by smaller herbivores, but the difference should be less marked than predicted simply on the basis of the body size–metabolic rate relationship. The question I will now consider is the extent to which this relation, based largely on artificial diets fed to captive animals, holds for free-ranging wild herbivores.

The first problem is to assess dietary quality. Ideally this should be expressed in terms of the concentration of available, i.e. both digestible and metabolizable, energy. However, digestibility is influenced by a number of factors, including plant species and part, stage of maturity, microbial activity in the fermentation chamber of the herbivore and rate of passage through it.

Protein concentrations are more readily measured than energy. Commonly dietary protein content is analyzed from samples of the food taken from the stomach or rumen. However, these results underestimate the protein concentrations in the ingested material, since more nutritious components pass out of the rumen more rapidly than slowly digesting fibrous material. For example, for topi the crude protein concentrations within food samples collected *via* an esophageal fistula averaged 2.7 percentage points higher than those analyzed in samples of rumen contents (Duncan 1975).

Nevertheless, the only comparative data available for a sufficiently wide range of species are those based on samples of rumen or stomach contents. The published data for crude protein concentrations in stomach contents show considerable variability, but much of this is related to whether or not the material was washed free of rumen liquor and associated microbes before analysis. If only washed samples are considered, there is a significantly negative correlation between crude protein contents and body mass for ruminants up to the size of African buffalo; but the value of the regression coefficient (-0.23 ± 0.07) is somewhat higher than that predicted allowing for variations in daily food intake (Fig. 6.1).

Megaherbivores exhibit protein levels in their stomach contents comparable to those of much smaller ruminants such as gazelles. For giraffe and black rhino this can be related to the predominance of dicotyledonous foliage in the diet, while elephants also include a high proportion of woody plant leaves in their diet during most seasons. Nevertheless the two grazing megaherbivores, white rhinos and hippos, apparently select diets no different in their protein concentrations from those eaten by most grazing bovids.

Some indication of digestible energy concentrations in the diet can be obtained from the rate of fermentation of the contents of the rumen, cecum or colon, assessed *in vitro* in terms of rates of gas production using samples

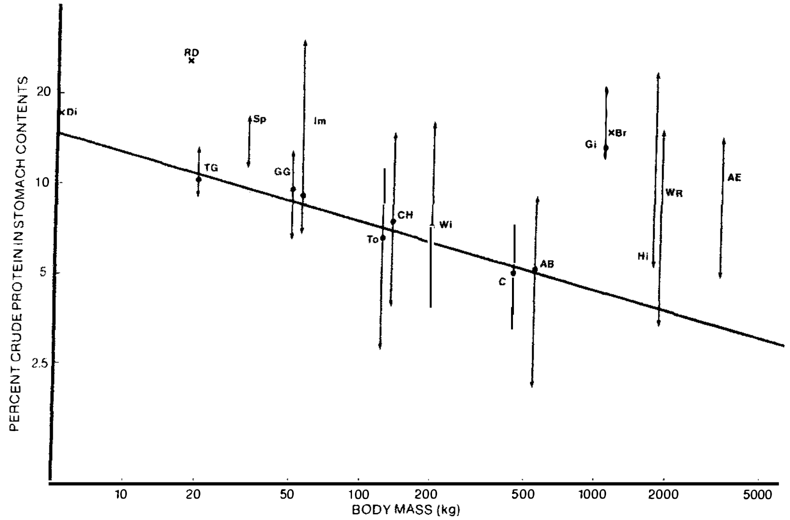


Fig. 6.1 Crude protein concentrations in the stomach contents of various large herbivores during the dry season in relation to body size. For key to species labels, see Appendix I. Data from Blankenship & Qvortrup (1974), Clemens & Maloiy (1982), Duncan (1975), Field & Blankenship (1973), Hall-Martin & Basson (1975), Hoppe *et al.* (1977a and b), Hoppe *et al.* (1981), Malpas (1977), Robinson (1979), Sinclair (1977) and Stanley-Price (1977); for white rhinos based on the crude protein contents of the grasses eaten, from Downing (1979) and Du Toit *et al.* (1940).

Regression line based on means for washed samples for ruminants only (as indicated by dots), excluding giraffe: CP (%) = $21.6M^{-0.23}$ (SE(b) = 0.028, $R^2 = 0.92$, $N = 9$, $P = 0.0002$).

from freshly killed animals. Hoppe (1977a) reported results obtained from 72 specimens of 11 species of wild ruminant collected during the African dry season. His findings show that rates of gas production decline as a function of $M^{-0.22}$, a very similar relation to that found for the variation in crude protein concentrations (Fig. 6.2). If this trend is extrapolated into the megaherbivore range, it is evident that African elephants exhibit high fermentation rates for their size; while hippos show exceptionally low fermentation rates. For elephants the high fermentation rate can be explained in terms of the high proportion of browse in their diet, since woody plant leaves tend to digest more rapidly than grass leaves (Owen-Smith 1982). No comparable data are available for any of the rhino species; but based on their rates of digestive turnover, rhinos would be expected to be intermediate between elephants and hippos, and hence to fall not very far from the projected regression line.

An alternative indication of dietary quality is in terms of the proportions of plant parts ingested. Bell (1971) and Jarman (1974) suggested that small

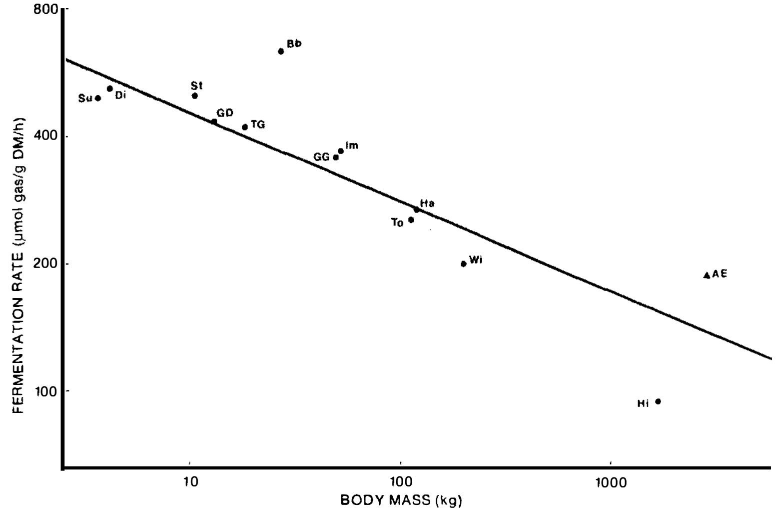


Fig. 6.2 Fermentation rates, expressed in terms of gas production, of rumen, cecal or colonic contents in relation to body mass. Circles = foregut fermenters, triangles = hindgut fermenters. Data from Hoppe (1977a), van Hoven (1977), van Hoven *et al.* (1981).
Regression, for ruminants only, as given by Hoppe (1977a): Digestive fermentation rate (μmole gas g $(DM)^{-1}h^{-1}$) = $945M^{-0.22}$ (SE(b) = 0.047, $R^2 = 0.695$, $N = 11$, $P < 0.05$).

ungulates are highly selective for the more nutritious plant parts, such as new leaves, flowers and fruits; while large ungulates are tolerant of a relatively high proportion of fibrous stems in their diets, although they seek out high quality plant parts when these are available. It is under dry season conditions that the metabolic tolerance of larger animals should be most clearly expressed. Hoppe (1977a and b) and others have reported the proportions of leaves, stems and other plant parts in the rumen or stomach contents of various large herbivores collected during the dry season. The fraction formed by non-stem material (i.e. leaves, leaf sheaths, flowers, fruits, whether from grasses or woody plants) declines significantly with increasing body mass (Fig. 6.3). Small antelopes like dikdik and grey duiker managed even in the dry season to secure diets containing 86–96% leaf material, 70–100% of which consisted of green leaf. In contrast, at this time of the year the rumens of medium-sized grazers, such as topi, hartebeest and wildebeest, contained only 28–46% grass leaf, only half of which was green. During the dry season of a drought year in Tanzania, elephant diets included about 55% wood, bark and roots, and only 38% leaf (Barnes 1982a).

The data reported above show that dietary quality does decline with

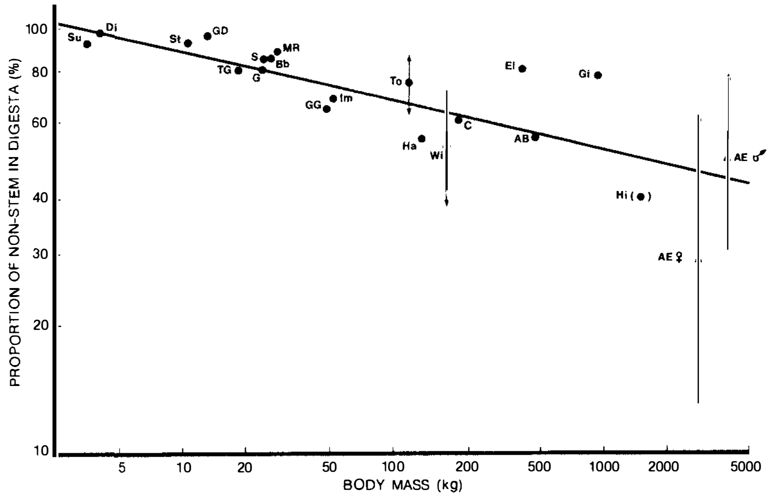


Fig. 6.3 Proportion of non-stem material (i.e. leaves, leaf sheaths, fruits, etc.) in the rumen or stomach contents of various large herbivores in relation to body mass (except for African elephants based on replicated food intake, and for hippos (bracketed) derived from fecal samples).
Circles = foregut fermenters, triangles = hindgut fermenters. Data from Barnes (1982a), Bell (1970), Berry (1980), Hall-Martin (1974), Hillman (1979), Hoppe (1977a and b), Irby (1977), Jarman & Sinclair (1979), Owaga (1975) and Scotcher *et al.* (1978).
Regression: % of non-stem material = $116M^{-0.118}$ (SE(b) = 0.018, R^2 = 0.721, N = 21, $P < 0.01$).

increasing body mass, despite some compensation in daily food intake. However, the wet season diets eaten by megaherbivores may differ little from those selected by medium-sized ruminants, at least as measured in terms of protein content. It is particularly during the dry season period of restricted herbage availability that the ability of very large herbivores to tolerate a low quality diet, characterized in particular by a high content of indigestible fiber, becomes evident.

On account of the metabolic rate–body size relation, larger animals lose condition more slowly on a submaintenance diet than do smaller animals (Bell 1971). Furthermore, Lindstedt and Boyce (1985) show that stored fat reserves become a greater fraction of body mass as size increases. Hence increased body mass could be an adaptation to compensate for extreme seasonal fluctuations in food availability. Notably, white rhinos may build up deposits of subcutaneous fat to aid their survival through the dry season. Selous (1899) commented that 'towards the end of the rainy season, in February and March, white rhinos used to become excessively fat, and would keep in good condition until late in the dry season. I have seen them so fat that between the skin and the flesh over the greater part of the body there was a layer of fat over one inch in thickness, whilst the whole belly was covered in fat to two inches thick.' The existence of similar fat deposits in the northern subspecies of white rhino was confirmed by Cave & Allbrook (1958). Hippos were renowned among early hunters for their fat, and Ledger's (1968) data show carcass fat contents for hippos of 7–11%, more than twice the mean value for African wild ruminants.

Foraging time

Bell (1971) suggested that, because larger herbivores have a greater absolute food requirement than smaller ones, they need to spend a somewhat larger proportion of the day eating than the latter. However, eating time depends on the rate of food intake obtained relative to body mass. If this rate varies in direct proportion to body mass then, since megaherbivores eat less food per day per unit of body mass than smaller ungulates, very large animals should be able to satisfy their nutritional needs within a shorter feeding time than that required by smaller species. Nevertheless, it was apparent in Chapter 4 that megaherbivores tend to forage for a greater proportion of their time than smaller ungulates. Thus we need to consider more critically the factors controlling food ingestion rate.

Food ingestion rate

Rates of food ingestion while feeding are a function of bite size, biting rates and the time spent apprehending or manipulating food items. Bite size is controlled by the width of the mouthparts used for plucking food and the extent of the gape, and by the depth of the bite taken. Biting rates are influenced by bite size, with large mouthfuls of food requiring more time to be chewed and swallowed than smaller ones. For giraffe, Pellew (1984c) found that these two factors tended to compensate, so that eating rates varied little despite a wide variation in the bite sizes obtained from different plant species. However, this does not hold for other browsing ungulates (Cooper & Owen-Smith 1986).

The proportion of time spent searching during foraging spells is related to the spatial dispersion of acceptable food items in the vegetation. If food items are fairly continuously distributed, so that some morsel can be located with nearly every advancing step, little time is diverted to searching; chewing and swallowing can be synchronized with stepping. If food items are patchily distributed, time must be spent walking from one patch to another, during which no eating occurs.

Bite dimensions should vary as a volume factor (width × gape extent ×

depth), provided that bite depth is not restricted by plant structure. However, a grazing ungulate cannot pluck more than the height of grass leaves available above ground level, whatever its potential bite depth. While browsers can remove complete leaves plus petioles from woody plants, a further increase in bite depth yields only the woody stem to which the leaves are attached. Thus plant structure can impose an upper limit on the bite depth that can be ingested – at least without incurring an abrupt increase in the fibrous content of the ingested material.

If the constraint imposed by plant structure on bite depth operated equally for large and small ungulates, bite dimensions would vary as an area factor. Rates of food ingestion per unit of body mass should then increase in relation to $M^{2/3}$, i.e. larger herbivores would need to feed for much longer than smaller ones in order to ingest the same proportion of their body mass. On the other hand, if bite depth was not a constraint (i.e. larger herbivores took proportionately deeper bites than smaller herbivores), then elephants and dikdiks could consume the same fraction of their body mass in the same eating time. However, dikdiks would have to forage for longer than elephants, because of the additional time they would need to search out the discontinuously distributed plant parts upon which they are dependent.

Rates of food ingestion are ultimately restricted by rates of digestive throughput. In the simplest physical model, the ruminoreticulum (or cecum, or stomach) can be envisaged as a container being emptied by a pipe (represented by the intestine). If the linear dimensions of the system were doubled, the volume of the container would be increased eight times, while the cross-sectional area of the pipe would be increased four times. If there was no compensating increase in the linear rate of flow of material through the pipe, it would then take twice as long to empty the container (ignoring frictional drag).

However, material can pass out of the gut either by passage along it (the slow route) or by absorption through the gut wall (the fast route). The fraction of material following either the one or the other pathway is dependent upon the digestibility of the diet. If dietary fiber contents increase with increasing body mass, rates of digestive throughput should decrease. Hence constraints of digestive passage should operate more severely on very large herbivores than on small herbivores.

Earlier it was found that megaherbivores ingested a lower fraction of their body mass per day than smaller ungulates. This could be the result either of a constraint on digestive throughput rates, due to lower dietary quality; or of their lower metabolic requirements, assuming similar quality diets. In either case, megaherbivores should be able to satisfy their quantita-

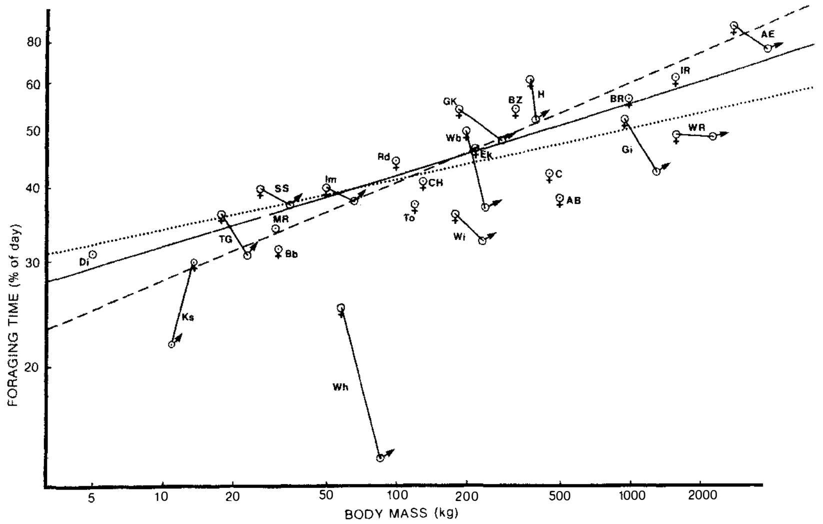


Fig. 6.4 Daily foraging budgets of large herbivores in relation to body mass. For key to species labels see Appendix I. Data from Clough & Hassam (1970), Craighead *et al.* (1973), Duncan (1975, 1980), Gogan (1973), Grimsdell & Field (1976), Grubb & Jewell (1974), Hendrichs & Hendrichs (1971), Hitchins (1971), Irby (1981), Jarman & Jarman (1973a), Laurie (1978), Low *et al.* (1981), Norton (1981), Novellie *et al.* (1984), Owen-Smith (1979), Pellew (1984b), Spinage (1969), Stanley-Price (1977), Thomson (1973), Walther (1973), Waser (1975) and Wyatt & Eltringham (1974).
Regression line for all species (solid): $FB(\%) = 24.2M^{0.12}$ ($SE(b) = 0.029$, $R^2 = 0.47$, $N = 21$, $P = 0.0006$); for ruminants only (dotted): $FB(\%) = 27.9M^{0.08}$ ($SE(b) = 0.026$, $R^2 = 0.46$, $N = 12$, $P = 0.0076$); for non-ruminants only (dashed): $FB(\%) = 19.0M^{0.17}$ ($SE(b) = 0.11$, $R^2 = 0.32$, $N = 7$, $P = 0.184$).

tive food requirements within a shorter daily feeding time than smaller species if plant structure did not restrict ingestion rate.

Foraging time budgets over the 24 hour diet cycle show a significant tendency to increase with increasing body mass (Fig. 6.4). Thus larger herbivores forage for longer per day than smaller species, despite lower food requirements and less time diverted to searching. Notably, white rhinos exhibit foraging times just as long as those of zebras, even though their specific food requirements are only one quarter as great as those of zebras.

Thus it is evident that plant structure does impose a restriction on food ingestion rate. However, the increase in daily feeding time with increased body mass is less steep than it would be if this constraint affected very large herbivores and small herbivores equally. We thus turn next to a consideration of possible adaptations in the mouth or other feeding structures that might compensate for a bite depth restriction. If bite depth is limited say by grass height, we need to examine the scaling of bite width in relation to body mass.

Mouth parts and other feeding structures

As an index of the scaling of bite width to body size, the ratio of effective mouth width, in mm, to the cube root of body mass, in kg, will be used. Among ruminants the effective mouth width is controlled by the breadth of the incisor tooth row, while for rhinos and hippos it is related to the width of the lips used for cropping grass. For a relatively broad-muzzled grazer like wildebeest, this index works out at 11.4, versus 7.0 for a narrow-muzzled browser like greater kudu (based on measurements kindly supplied by N. Caithness). For a white rhino with a bite width of 200 mm, the bite width index comes to 17.1; while for hippos with a bite width of nearly 0.5 m (Laws 1981a) the index works out at about 35. The 50% increase in the effective bite width of white rhinos over wildebeest would be sufficient to reduce the foraging time needed by white rhinos to ingest a similar fraction of their body mass by about one third. If both animal species were equally constrained by grass height in their bite depth (i.e. eating rates were a function of $M^{2/3}$), a 1600 kg white rhino would need to feed for 1.3 times as long as a 180 kg wildebeest to ingest the same fraction of its body mass – instead of twice as long, as would be the case without the compensating expansion of bite width. A hippo with its even wider mouth would need to feed for only two-thirds as long as a wildebeest for the same specific food intake. In fact wildebeest feed for about 8 hours per day (Berry *et al.* 1982), as also do hippos, compared with 12 hours per day for white rhinos. This suggests that effective bite gape must also be constrained, taking into account the lower quantitative food requirements of the megaherbivores relative to wildebeest.

An elephant has a very different feeding adaptation in the form of its mobile trunk, which enables it to pluck large amounts of herbage at a time. For African elephants the mean weight of food gathered per trunk-load was 75 g (wet mass) in a Zimbabwean woodland (Guy 1975), while for Asian elephants in Sri Lanka an average weight of 150 g per trunk-load was calculated (Vancuylenberg 1977). Converted to dry mass this represents 10×10^{-6} to 20×10^{-6} of body mass. For cattle the mean bite mass of 0.33 g (dry weight) (Chacon & Stobbs 1976; Zimmerman 1978) represents 0.8×10^{-6} of body mass, i.e. only 4–8% as much.

However, the plucking rate of an elephant in terms of trunk-loads per minute is very much less than the biting rates achieved by cattle and other ungulates. The feeding rate of African elephants in Zimbabwe averaged 2.4

trunk-loads per minute (Guy 1975). Feeding rates of 5.9 trunk-loads per minute were recorded in Uganda (Wyatt and Eltringham, 1974), while in Tanzania feeding rates decreased from 8.4 trunk-loads per minute during the wet season to 3.1 trunk-loads per minute in the dry season (Barnes, 1979). For Asian elephants feeding rates of 2.1 trunk-loads per minute and 0.9 trunk-loads per minute were found by McKay (1973) and Vancuylenberg (1977) respectively, in the same park in Sri Lanka. In Malaya a feeding rate of 0.9 trunk-loads per minute was recorded (Olivier 1978, cited by Eltringham, 1982).

Based on Guy's data for a predominantly woody browse diet, the mean food ingestion rate of African elephants is about 72 g dry mass per minute, equivalent to 24×10^{-6} of body mass. For cattle with a biting rate of 55 per minute (Chacon & Stobbs 1976; Zimmerman 1978), the food ingestion rate amounts to 45×10^{-6} of body mass. Thus the large amount of herbage plucked per trunk-load by elephants is not quite adequate to compensate for the slower plucking rate.

To achieve the same mass-specific food intake as cattle, elephants would need to feed for nearly twice as long. However, the daily food requirement of an elephant per unit of body mass is only about 55% of the food intake of cattle. This reduced food intake rate almost exactly compensates for the reduced daily food requirement, so that elephants should be able to satisfy their appetite within about the same feeding time as cattle. However, the daily foraging times recorded for African elephants by Wyatt & Eltringham (1974) in the Queen Elizabeth National Park in Uganda were about 50–80% longer than those typically shown by cattle. This suggests that these elephants, occupying a largely grassland area, were in less favorable habitat than those studied by Guy (1975) in mopane woodlands in Zimbabwe.

Grazers and browsers

Notably most of the species falling above the regression line of daily foraging time on body mass (Fig. 6.4) are browsers or mixed feeders, while those falling below the line are grazers (with the exception of bushbuck). This pattern can be explained on the basis of the patchy distribution of woody plants compared with the even spread of grasses. For example, black rhinos spend about 20% of their day walking (Goddard 1970a), compared with only 7% for white rhinos (my study). Black rhinos feed for about 30% of the daylight hours, so that their food ingestion rate is reduced by about one third relative to white rhinos due to this effect. Likewise browsing kudus spend about 70% of their foraging time actually feeding (Owen-Smith & Novellie 1982), compared with 85–90% for largely grazing impalas (Dunham 1982).

Males and females

For most ungulates for which separate data for the two sexes are available, females forage for longer than males (Fig. 6.4). A similar pattern exists among primates (Clutton-Brock & Harvey 1977b). This difference follows from the additional nutritional demands imposed on females by pregnancy and lactation. Thus females generally need either to eat relatively more food per day than males, or to seek out higher quality food than that acceptable to males. Lactating females show higher stomach fills than non-lactating females both for hippos (Laws 1968b) and for African elephants (Laws *et al.* 1975). However, no data seem to be available to indicate whether females usually ingest more protein-rich food than males.

For white rhinos there is no sex difference in foraging budgets. White rhino males need just as long to satisfy their food requirements as females. This may be an outcome of the constraint imposed by grass height, i.e. white rhino males cannot increase their bite depth in proportion to their increased body size relative to females.

Diurnal and nocturnal feeding

The trend towards increasing foraging times with increasing body mass is apparent only in data based on the complete 24 hour cycle. Foraging times for the daylight hours alone show no obvious trend. The ratio of night-time to daytime feeding, for species from the size of Thomson's gazelle upwards, shows a downward trend with increasing body mass (with giraffe anomalous) (Fig. 6.5). Extreme examples, which cannot be denoted in the graph, include (i) warthogs, which feed for nearly half the day but spend the entire night hidden away in burrows (Cumming 1975); (ii) hippos, which remain inactive in pools during the day, and carry out all of their foraging at night. Moreover, megaherbivores generally travel to and from water after nightfall, while most medium-sized ungulates drink during the day.

However, very small antelope, like grysbok, grey duiker and suni, are more active at night than during the day (Novellie *et al.* 1984; T. Allan-Rowlandson personal communication; R. H. V. Bell personal communication), as also are both mountain and common reedbuck (Irby 1981, and

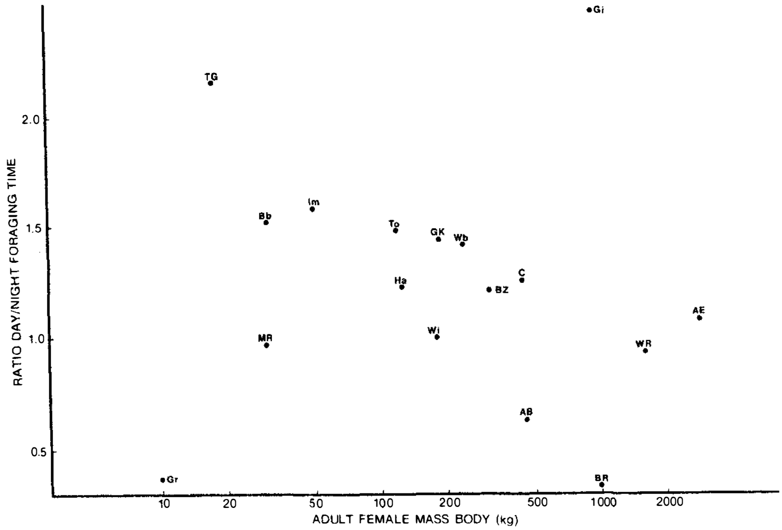


Fig. 6.5 Ratio of daytime to night-time feeding in relation to body mass. Data from references given in caption of Fig. 6.4 (excluding giraffe, $N = 14$, $R^2 = 0.442$, $P < 0.1$).

personal observations). These are all cryptic species relying on concealment for predator evasion. Medium-sized antelope such as impala feed for nearly one third of the night, but move around much less while doing so than during the day, and tend to congregate in open areas during the hours of darkness (Jarman & Jarman 1973a). Megaherbivores, being relatively invulnerable to predators, can afford to move around more at night than can smaller species. African buffalo, which are also more nocturnal than diurnal, probably gain some advantage in terms of predator protection from their very large, compact herd structure even at night.

Thermoregulatory constraints

Another factor promoting increased nocturnal activity by megaherbivores is the problem of maintaining thermal equilibrium. Maintenance metabolic rates are adjusted nearly in proportion to the surface area available for dissipating body heat. But besides body maintenance, the additional heat generated during muscular activity also needs to be taken into account.

Locomotion costs less energy per unit distance covered for big animals than for small animals (Taylor 1973). This is only because small animals need to take more steps to cover the same distance. A wide variety of data on the energy expended in running, flying and swimming support a hypothesis that all animals require the same quantity of energy in joules per unit of body mass to move one step (Gold, 1973). However, because the mass-specific resting metabolic rate decreases with increasing body mass, the costs of movement relative to maintenance metabolism are greater in larger animals than in smaller animals (Garland 1983; Peters 1983).

White rhinos averaged 35 steps per minute while walking, while 50 steps per minute were recorded for greater kudu females weighing 180 kg (Owen-Smith & Novellie 1982). Thus a white rhino should be expending only about two thirds as much energy per unit of walking time, relative to its body mass, as a kudu. However, relative to its basal metabolic rate the white rhino would be expending three times as much energy. Assuming both animal species to be constructed as simple cylinders, the ratio of surface area to volume for a 1600 kg white rhino is only about half that for a 180 kg kudu. Thus white rhinos have a smaller surface area available to dissipate the excess body heat produced by this activity than do kudus. Hence the problem of getting rid of the excess body heat produced during periods of muscular activity is more acute for megaherbivores than for smaller ungulates.

Accordingly, it is advantageous for megaherbivores to be more active at night, when there is less environmental heat load, than during the day. In fact, white rhinos and elephants might tend to perform all their feeding during the night, were it not for the constraints imposed by food ingestion and digestion rates. Black rhinos are much more nocturnal than white rhinos, probably as a consequence of the more rapid fermentation of browse leaves compared with grasses. Hippos are able to do all of their feeding at night, on account of the enhanced food ingestion rate conferred by their very large mouths.

The lack of hair on extant megaherbivores is also an aid to heat dissipation. Any liquid applied to the bare skin, whether in the form of water or mud, assists the cooling process. Observations that rhinos wallow at night as well as during the day support the hypothesis that it is the extra heat load generated by muscular activity that creates special problems for megaherbivores. Notably, white rhinos also possess unusually large sweat glands distributed over the whole body surface, evidently an adaptation for the rapid release of liquid for emergency cooling (Cave & Allbrook 1958). Elephants have a special adaptation in their enormous ear pinnae, which serve as heat radiating surfaces. Blood leaving the ear is notably cooler than that entering it (Buss & Estes 1971). It is this feature that allows African elephants to forage for as long as 9 hours during the daytime even in tropical African climates.

Summary

Daily foraging time shows a tendency to increase with increasing body mass, suggesting that bite size and hence feeding rate is constrained by features of plant structure. Megaherbivores exhibit compensatory adaptations to counter this restriction, either in terms of exceptionally wide mouths, or in the form of a special feeding apparatus such as the elephant's trunk. Foraging time budgets are also influenced by: (i) food type – browsers spend more time walking between feeding stations than grazers of similar body mass, and hence need to forage for longer; (ii) digestive passage rates – these constrain feeding times less in browsers than in grazers, and less in equids compared with other ungulates; (iii) reproductive status – pregnant or lactating females forage for longer than males or non-pregnant females; (iv) predation risks – smaller species in open habitats forage less at night than during the day; (v) heat balance related to muscular exertion – megaherbivores require special adaptations for dissipating body heat to allow them to forage for a large part of the day.

Home range extent

Megaherbivores tend to cover larger home ranges than smaller ungulates. McNab (1963) proposed that home range extent was directly dependant on bioenergetic requirements, i.e. it should vary in relation to $M^{0.75}$. However, Harestad & Bunnell (1979), using data drawn mostly from North American mammals, found that the power coefficient b relating home range area to body mass was significantly greater than 0.75; for herbivores (including squirrels and other granivores) they found $b = 1.02$, while for carnivores $b = 1.36$. For primate home ranges, Milton & May (1976) and Clutton-Brock & Harvey (1977a) found values for b of 0.83–0.99 for frugivores and 1.06–1.15 for folivores. Harestad & Bunnell (1979) explained the discrepancy with the suggestion that mean resource density within the home range decreased with increasing body size, because larger home ranges tended to include more lacunae or patches of low productivity.

Clutton-Brock & Harvey (1977b) pointed out that home range size should be related to total energy requirements, including expenditures for activities, rather than to resting metabolic rate. However, data for primates (Harvey & Clutton-Brock 1981), and for combined samples of birds and rodents (Mace & Harvey 1983), show that home range size increases in

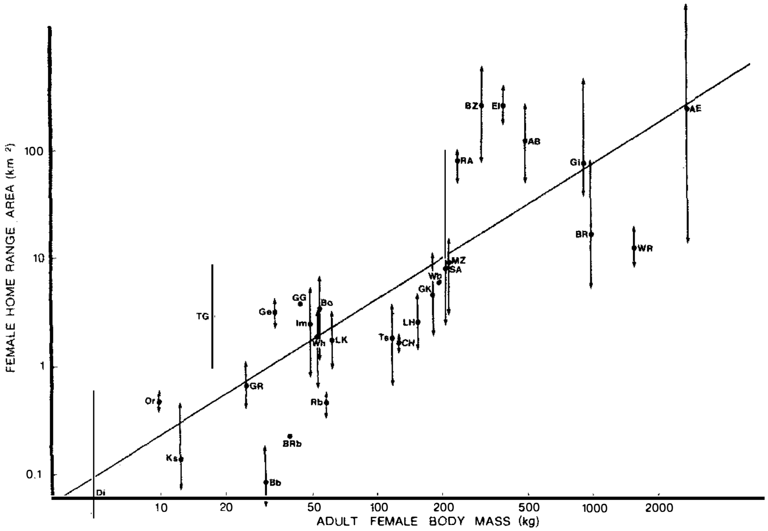


Fig. 6.6 Female home range extents for African large herbivores in relation to body mass. Key to species labels in Appendix I. Data from Cumming (1975), David (1973), Douglas-Hamilton (1972), Dowsett (1966), Dunbar & Dunbar (1974), Estes & Estes (1974), Goddard (1967), Gosling (1974), Grobler (1974), Hendrichs & Hendrichs (1971), Hillman (1979), Hitchins (1971), Jarman & Jarman (1973a), E. Joubert (1972), S. Joubert (1972, 1974), Jungius (1971b), Leuthold (1970, 1971, 1972 and 1974), Leuthold & Sale (1973), Leuthold & Leuthold (1978), Langman (1973), Murray (1980), Owen-Smith (1979), Pellew (1981), Simpson (1974), Sinclair (1977), Spinage (1969), Walther (1964, 1965), Waser (1974). Regression based on the geometric means of the figures reported from different localities (indicated by dots). Lines indicate the complete range of published data.
Regression line: $HR(\text{ha}) = 1.35M^{1.25}$ (SE(b) $= 0.16$, $R^2 = 0.70$, $N = 29$, $P = 0.0001$).

relation to daily metabolic expenditure raised to the power 2.2, rather than 1.0. In effect, larger animals require disproportionately larger home ranges than can be explained simply on the basis of energy requirements.

Damuth (1981a) suggested an alternative hypothesis. He pointed out that the extent of home range overlap increases with increasing body size, and that this effect could account for the observed departure from the metabolic rate–body size relation.

For most African ungulates only female home ranges can be related directly to nutritional requirements, because male home ranges are restricted by social pressures. The data show that the total extent of the home ranges covered by adult female ungulates increases more steeply with body mass than was found for North American herbivores, with an estimate for the power coefficient *b* of 1.25 ± 0.32 (Fig. 6.6). Notably the species falling above the regression line tend to be those forming large herds, for example Thomson's gazelle, African buffalo and eland; while solitary species like white rhino fall below the line. Sociality is more prevalent among larger ungulates than among smaller species (Jarman 1974); and the need to move over a relatively larger area can be viewed as a cost of sharing the home range with companions.

In terms of resource requirements it is more appropriate to divide the home range area by the size of the social group, to obtain the home range extent available per individual. For this purpose the social group represents not the number of animals associated together at any one time, but rather those individuals sharing a common home range. For example, impala females form clans of 50–100 animals occupying fairly discrete areas covering 0.8–1.8 km^2 (Murray 1982b). African elephants likewise form clans of 100 or more individuals sharing a common home range of about 200–700 km^2, with little overlap between different clan areas (Martin 1978 and personal communication; Hall-Martin 1984). For white rhinos no such clan organization exists, so that it is impossible to draw a direct comparison with other species on this basis. If a typical group size of three is assumed, then the home range area per individual white rhino is about 4 km^2. However, the population density of 5.3 per km^2 prevailing in the Madlozi study area indicates that the actual extent of habitat available to each individual white rhino was only about 0.2 km^2.

The regression of home range extent per individual against body mass yields an estimate for *b* of 0.83 ± 0.43, which is not significantly different from 0.75 (Fig. 6.7). However, this analysis does not allow for range overlap between social units. Home ranges tend to be fairly discrete among the smallest antelope species, among which females frequently share the territories of individual males. Among the larger ungulates a pattern of overlapping home ranges between different female groups is usual.

Home range size thus represents a compromise between individual metabolic requirements and social pressures, so that no simple functional relationship with body size should be expected (Damuth 1981a). Metabolic demands increase with body mass, but so does group size, and also the degree of range overlap between different individuals or groups. Bioenergetic influences are better revealed by the relationship between prevailing population densities and body mass. This approach will be taken up in Chapter 14 when body size relationships at the demographic level are considered.

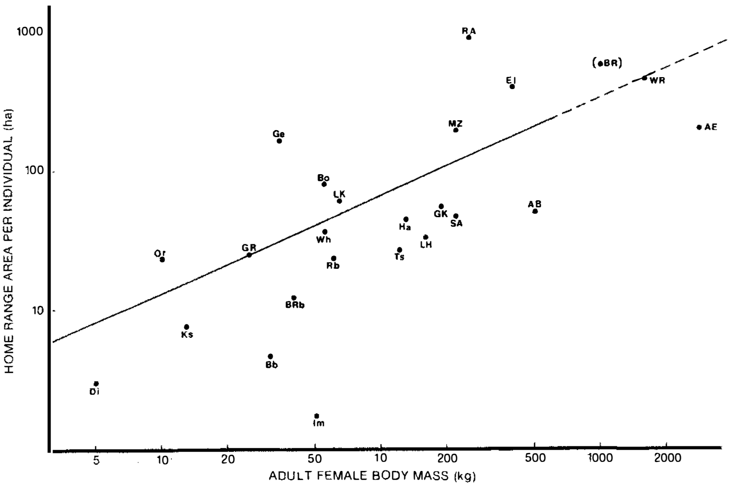


Fig. 6.7 Home range extent per individual for African large herbivores in relation to body mass. Based on dividing the home range extent by the size of the social group. Key to species labels in Appendix I. References as in Fig. 6.6. Regression line (excluding megaherbivores): $HRI(\text{ha}) = 1.07M^{0.83}$ (SE(b) = 0.21, $R^2 = 0.44$, $N = 21$, $P = 0.001$).

Trophic ecology of megaherbivores: summary

Let me now summarise the general findings of both this chapter and the previous one concerning the trophic adaptations of megaherbivores. Large body size automatically confers an advantage in terms of ability to digest structural cellulose through bacterial fermentation, due to a prolonged retention time of food in the gut. It thus represents an alternative mechanism for enhancing cell wall digestion to the development of delaying compartments in regions of the gut as shown by the ruminant artiodactyls. However, the digestive efficiency achieved through large size does not quite match that attained by certain grazing ruminants. This is because megaherbivores lack the ability to remasticate the ingested forage and thereby increase the surface area for bacterial action, which is a major advantage of the ruminant digestive system.

The increase in fermentative degradation of cell wall that occurs with increasing body size is probably the basic explanation for the trends towards large size shown repeatedly among lineages of hindgut fermenters. The two grazing rhinos epitomize this solution to the problem of being a herbivore, while hippos show that similar results can be achieved using a foregut fermentative chamber.

An alternative adaptive route open to hindgut fermenters is to compensate for digestive inefficiency through high food intake. What is quickly digestible is digested, and the remainder is passed out of the gut to make way for more material. This is the solution adopted by equids, and by small hindgut fermenters such as lagomorphs and certain rodents. Such species select 'duplex' food sources consisting of a suitable mix of quickly fermentable carbohydrates with completely indigestible fiber. For example, zebras consume a mixture of green grass leaves diluted by fibrous stem, while similar-sized ruminants filter out some of the structural fiber using the selective apprehension ability conferred by their lower incisor-palatal bite. Compared to modern rhinos, both extant species of elephant tend towards the equid pattern. When feeding on grasses in the dry season, they tend to select underground parts where carbohydrates are stored, rather than trying to digest the fibrous dry leaves, as white rhinos do. This follows from the fact that both African and Asian elephants are adapted as mixed grazer–browsers, and woody plant branchlets offer a suitable mix of rapidly digesting leaves and indigestible stems. In fact, African elephants frequently discard poor quality leaves in favor of bark containing some fraction of soluble carbohydrates. The extinct mammoths and grazing gomphotheres such as *Stegomastodon*, which from their dentition were adapted for a diet of fine grass leaves, most probably resembled the grazing rhinos in having a relatively efficient hindgut fermentation.

Megaherbivores following the rhino digestive solution are restricted in their food intake by the inherently slow rate of passage of digesta through their gut. They are thus dependent upon a high enough concentration of fermentable fiber in their diet to achieve both an adequate throughput rate and a sufficient level of digestible energy. The result of the interaction between these two factors is that, despite their much lower metabolic demands per unit of body mass, such species are dependent on a dietary quality not that much lower than that needed by much smaller ruminants, to satisfy their maintenance requirements. Thus, during the dry season white rhinos occupy regions where the soil nutrient–rainfall combination causes grasses to build up only moderate levels of indigestible fiber in their leaves (so-called 'sweetveld' conditions, as prevalent at Umfolozi). In 'sourveld' regions, where grasses are mostly highly fibrous and lack nutrients in above-ground parts during the dry season, white rhinos feed mostly in those areas of the landscape where soil nutrients accumulate, for example around termitaria and along the margins of drainage sump grasslands (which was a feature of much of their former distribution in Zimbabwe). The northern steppe-tundra favored by the extinct woolly mammoths was characterized by a combination of low precipitation and fertile loess soils, and so was a boreal counterpart of southern African sweetveld. Nevertheless, under submaintenance conditions during the dormant season for plant growth, all megaherbivores can survive somewhat longer on a starvation diet than would be the case for smaller animals with a higher metabolic rate.

Relatively nutritious vegetation components tend to be available at a somewhat low standing biomass. Thus megaherbivores dependent upon such vegetation encounter problems in achieving an adequate rate of food ingestion relative to their needs. Their ability to compensate through increased foraging time is restricted by problems of thermoregulation, exacerbated by the heat generated through muscular activity relative to their restricted surface area to muscular mass ratio. Thus they need adaptive modifications of food gathering structures to compensate for the limitations imposed by plant growth patterns. In grazing rhinos and hippos, this is achieved by expansions of the lips. Interestingly, mammoths exhibited flanges on the sides of the trunktip, which probably served to increase the amount of grass that could be lifted per trunk-load (Guthrie 1982).

7

Social organization and behavior

Introduction

Patterns of social organization reflect the cooperative and competitive interactions occurring among animals within local populations relating to survival and reproduction. Generally different age/sex classes differ in their spatial dispersion, i.e. group membership and the spatial relationships both within and between groups. Other social relationships may be evident from the patterns of behavior displayed in encounters, for example those signifying dominant/subordinate relations. Dominance is particularly a feature of adult males, which are inevitably competitors for reproductive opportunities. Females in turn may exert some selection over the sire of their offspring. Anti-predator responses are also appropriately considered in this chapter, since the affiliative relationships established among adult females serve largely to reduce the risks of predation, not only for self but also for progeny.

Group structure

The term group refers to a close spatial association between individuals. However, socially the temporal cohesion of the group is relatively more important than short-term spatial proximity. Groups may vary in size, and in the age/sex classes of animals composing them. Different groups may either move independently of one another, or tend to associate together, or space themselves out with respect to other groups. Grouping patterns may furthermore change seasonally, particularly in relation to variations in reproductive activity.

Elephants

Among African elephants, the nuclear group comprises an adult female together with 1–3 immature progeny of varying ages. However, generally one finds 2–4 mothers plus young associated together to form

Fig. 7.1 African elephant family unit (photo courtesy N. Leader-Williams).

family units typically numbering about 4 to 12 animals (Fig. 7.1). From an analysis of the ages of the animals (determined from culling operations), many of these units evidently consist of an old female or matriarch (aged 38–60 years) together with her mature daughters and their offspring. Other family units include two mature females of similar age, which may be sisters. While members of family units are usually found close together, they may separate into nuclear mother–young units under dry season or drought conditions. When alarmed family unit members bunch around the matriarch, and if she is shot they mill around in confusion. The few solitary females encountered are almost invariably senile individuals over 50 years in age. Groups recorded for forest elephants are somewhat smaller than those typical of savanna elephants. In the Tai National Park, Ivory Coast, the mean group size was 3.4 (maximum 9), and solitary females were not unusual.

Different family units are commonly found in close proximity, within a kilometer or less, and tend to move in a coordinated fashion along parallel lines. Large aggregations of elephants numbering 100–1300 animals, including a number of males, may also be observed during the wet season, and these may maintain cohesion over several weeks. Radio-telemetric monitoring of movements in the Sengwa Research Area in Zimbabwe indicated the existence of distinct clans of females plus young, including a hundred or more animals. While the ranges of neighboring clans overlap peripherally, members of different clans are seldom in the overlap area at the same time. The very large herds of a thousand or more elephants observed in the Murchison Falls Park in Uganda during the 1960s could have been a result of the compression of clans by human settlements occupying part of their former range (Barnes 1982b; Buss & Savidge 1966; Douglas-Hamilton 1972; Hendrichs 1971; Laws 1969b, 1974; Laws, Parker & Johnstone 1975; Leuthold 1976b; Martin 1978; Merz 1986b; Moss 1983; Western & Lindsay 1984; Wing & Buss 1970).

Males over 16 years of age associate only transiently with the family units. Bulls join together in groups averaging 2–4 animals (maximum 35, although there is one report of a group of 144 bulls from the Tsavo region of Kenya). Associations between particular individuals are temporary. The longest recorded attachment lasted 51 days, but most bulls remain together only a day or two. Between 13% and 60% of adult males are solitary, the proportion tending to be highest during the wet season. Adult males favor so-called bull areas distinct from the home ranges of female clans, but wander widely at certain times (Barnes 1982; Croze 1974a; Hall-Martin 1984; Hendrichs 1971; Laws 1969; Laws, Parker & Johnstone 1975; Martin 1978; Moss 1983).

Asian elephants show a grouping pattern similar to that of African elephants, although population levels are too low for large aggregations to form. In Sri Lanka the modal group size of female–young units is 2–5, with the largest recorded groups numbering 39 animals at Gal Oya and 71 at Amparai (but there is a report of a herd of 150 from elsewhere in Sri Lanka). Large herds generally split into smaller foraging groups, which move in a coordinated manner. Infrasonic calls may help maintain coordination between subgroups separated by distances of several kilometers (and have recently been confirmed also for African elephants). So-called herds comprising between 20 and 150 animals occupied fairly discrete home ranges.

About 70–80% of Asian elephant bulls are solitary, although groups of up to 7 males form occasionally. Bulls may join family units, but remain in their company for only a few days before departing (Eisenberg, McKay & Jainudeen 1971; Ishwaran 1981; Kurt 1974; McKay 1973; Payne, Langbauer & Thomas 1986; Santiapillai, Chambers & Ishwaran 1984).

Hippopotamus

Hippos congregate in their daytime refuge pools in discrete groups typically numbering 10–30 animals. These generally include a large dominant bull, several females and young, and from two to six peripheral males.

Such groups appear to remain fairly constant in their membership, at least over periods of a month or two. However, when rivers dry up animals may be forced together in aggregations of up to 150 animals in remaining pools. Solitary males commonly occupy outlying small pools, although sometimes all-male groups may share a pool. Hippos travel solitarily while feeding on land at night, except for females accompanied by one or more offspring (Marshall & Sayer 1976; Olivier & Laurie 1974; Verheyen 1954; Viljoen 1980).

Giraffe

Giraffe females and young form groups averaging between 3 and 17 animals in different areas. A maximum group size of 239 was recorded in the Serengeti, but no group larger than 35 has been reported elsewhere. However, observers vary in the spatial limits they use in identifying groups, some regarding all animals within less than a kilometer as being part of the same group (which is reasonable considering the wide visual field that a giraffe commands from its height). Groupings are not cohesive, but change in composition from day to day. Female home ranges overlap extensively. Individual females return repeatedly to the same localities to give birth, even when their home ranges have shifted away from these areas.

Adult male giraffe are most commonly solitary. However they may join female groups temporarily, or associate in loose all-male groups. Male home ranges also show much overlap (Foster & Dagg 1972; Hall-Martin 1975; Langman 1977; B. M. Leuthold 1979; Pellew 1983a).

Rhinoceroses

For Indian rhinos the cow-calf unit is the only enduring association. The largest recorded groups comprised 3 animals, but such associations rarely persisted longer than 2–3 days. Adult males are solitary, apart from temporary associations with females. Sixty-three percent of subadults were recorded alone, the remainder being associated with another subadult. Home ranges show much overlap, both between bulls and cows as well as between different individuals of each sex (Laurie 1982). Javan rhinos and Sumatran rhinos are likewise mostly solitary in their habits (Borner 1979; Groves & Kurt 1972; Schenkel & Schenkel-Hulliger 1969b).

Black rhino females were solitary or accompanied only by a calf in 75% of sightings at Ngorongoro and Olduvai in Tanzania, while 80% of the bulls seen were solitary. Subadults were solitary in about 40% of sightings at Ngorongoro and 68% of sightings at Olduvai. Only 1.7% of black rhino groups at Hluhluwe consisted of more than 3 animals, the largest association numbering 7 animals. The largest group recorded at Ngorongoro consisted of 5 animals – 2 cows, a calf, a subadult female and a bull – but these animals remained together only four days. One temporary aggregation of 13 animals disbanded after two hours. The largest group recorded at Amboseli, Kenya, consisted of four animals: an old cow, a young cow, a subadult female and a bull (Goddard 1967; P. M. Hitchins personal communication; Klingel & Klingel 1966; Schenkel & Schenkel-Hulliger 1969a).

Radio-telemetric tracking of black rhinos at Hluhluwe showed that female home ranges overlapped; while adult males occupied mutually exclusive home ranges, except for a case in which two bulls shared the same range. In Namibia no two bulls shared the same home range. Elsewhere extensive overlap between the home ranges of both males and females has been reported, but the possibility of dominant and subordinate bulls sharing home ranges was not considered, nor was allowance made for the possibility of bulls leaving their home area to travel to and from water (Goddard 1967; Hitchins 1971; Joubert & Eloff 1971; Schenkel 1966).

White rhinoceros

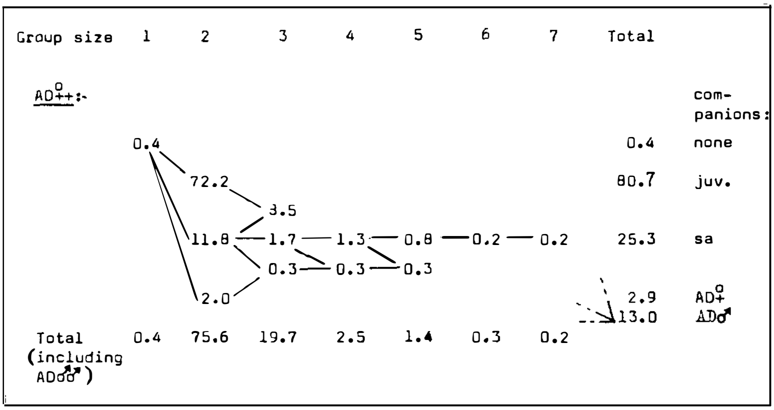
My observations on white rhinos were based on animals that were individually identifiable, from variations in horn shapes and other features. At Umfolozi most white rhino cows were accompanied only by a single offspring; while white rhino bulls were most often solitary (Fig. 7.2). Subadults tended to be associated in pairs, either of the same or opposite sex. Groups of three generally consisted of either a subadult attached to a cow–calf pair, or an adult male accompanying a cow plus calf. A few groups comprised three or more subadults, including in some instances a cow lacking a calf. The largest cohesive group in the study area numbered seven animals, a cow and six young subadults. One group of nine subadults was seen outside the study area. Most of the larger groups represented temporary associations, and broke up into units of two or three within a few days.

A few groups included two adult females, both without calves. In most of these cases one of the females was a young adult that may have been an offspring of the older cow. In one case both females were in early prime and of closely similar age, so that a mother–offspring relation was precluded. These two cows remained together, along with 2–3 adolescent companions, for four months, until one of them gave birth. The bond between the two cows was quite amicable, with no dominance or leadership difference expressed.

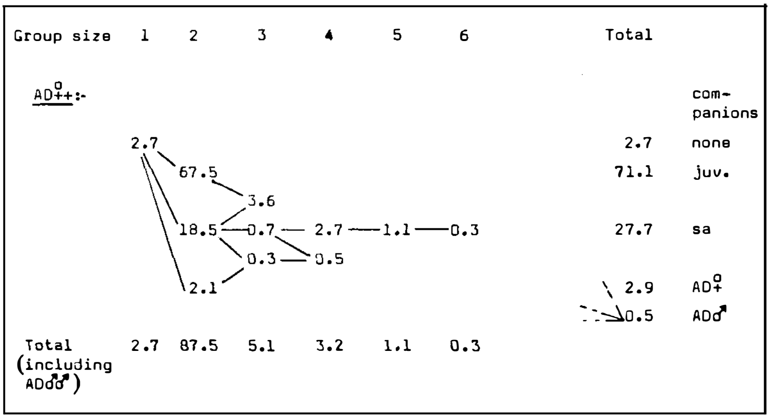
Cow–calf pairs as well as pairs of subadults tended to keep close together, generally within one body length (about 4 m). A subadult or second adult

(a) Cows

(i) All groups



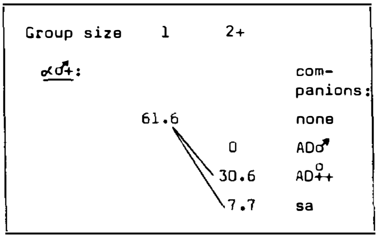
(ii) Stable associations



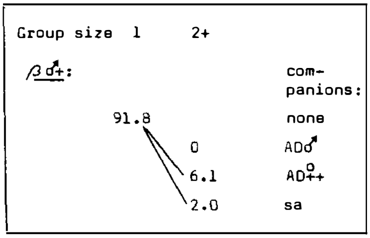
(b) Adult ♂♂

(i) All groups

α♂♂

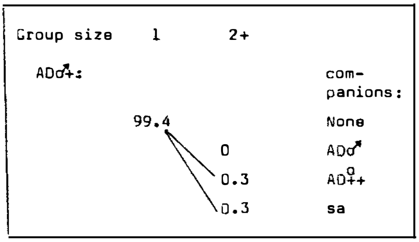


β♂♂



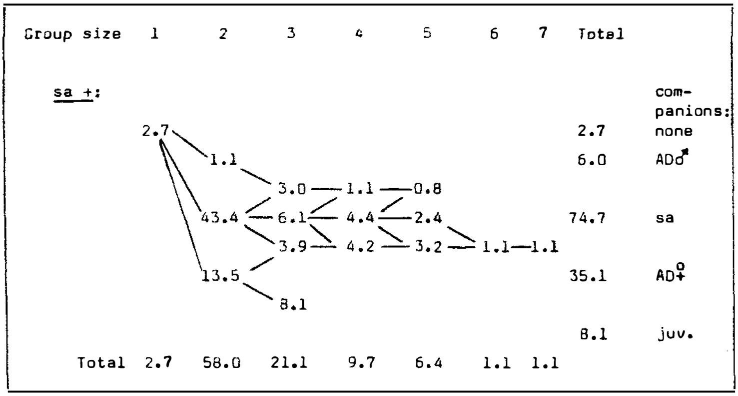
(ii) Stable associations

all AD♂♂*



(c) Subadults

(i) All groups



(ii) Stable associations

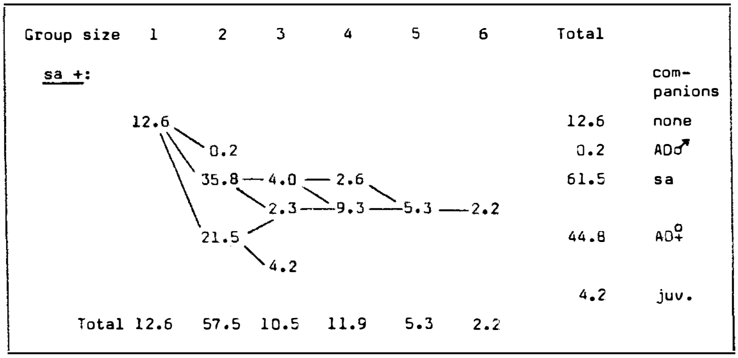


Fig. 7.2 Grouping patterns of white rhinos at Umfolozi. Figures represent the percentage of individuals of each age/sex category that were associated with each combination of group size and age/sex class of companions. Lines clarify successive additions in building up larger groups. Results are analyzed separately for stable associations, i.e. groupings persisting for longer than a month. For all groups, N = 1432 records; for stable associations, N = 935 records, α♂♂ = territorial adult males, β♂♂ = subordinate adult males. From Owen-Smith 1975.

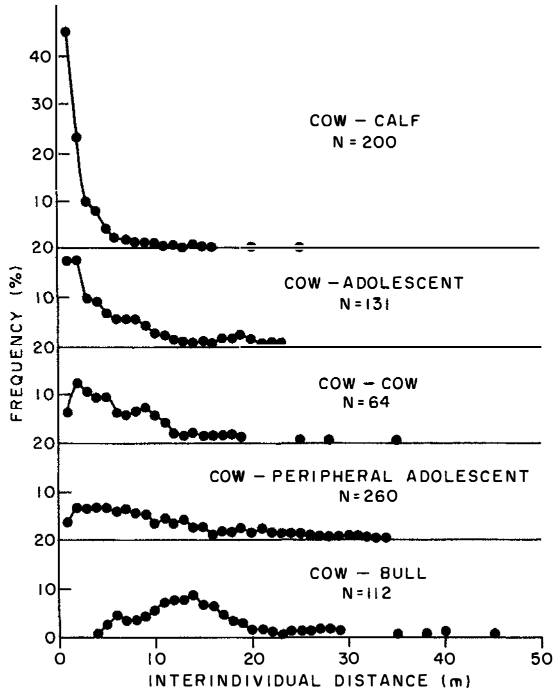


Fig. 7.3 Frequency distribution of interindividual distances in different white rhino groupings.

female attached to a cow maintained somewhat greater spacing, while a bull accompanying a cow tended to lag about 15 m behind her (Fig. 7.3).

White rhino cows generally responded neutrally when they met. They grazed in the same areas, and lay close together at restplaces, without antagonism. Sometimes cows approached one another to make nasonasal contact, and about a quarter of these meetings developed into playful horn sparring. In one instance a prolonged but playful horn wrestling and chasing game developed between two cows, with the subadult companions of both cows also joining in. In a small proportion of meetings cows exchanged threatening snorts or roars, usually in circumstances where one was accompanied by a young calf. Cows also exchanged aggressive roars and snorts at waterholes, where animals from different areas came into close proximity.

The home ranges of white rhino cows were individually distinctive but overlapped extensively. There was no indication of clans sharing a common home range. Nevertheless, there appeared to be some subdivision of the population with regard to the use of particular waterholes. None of the study area cows was recorded south of a spring located at the southern limit of the study area, while few of the cows seen to the south of the spring appeared in the study area.

Summary

Elephants of both species are highly social, showing a hierarchical pattern of groupings including mother–offspring associations, extended family units and coordinated aggregations of a hundred or more animals. Distinct clans of females plus young occupy fairly discrete home ranges. Adult males may be either solitary, associated in small all-male groups, or attached to female units. Hippos associate together in groups, including several females plus young and one or more males, in their refuge pools; but animals forage solitarily on land at night. Giraffe females form small groups which change in composition from day to day; while males are solitary or in small all-male groups. Rhinoceroses of all species are generally solitary. Cohesive groups consist mostly of mother–offspring associations, or of pairs formed between subadults. Among Indian rhinos and black rhinos subadults are found alone more often than not. In contrast white rhino subadults generally join together in pairs or larger groups, while cows without calves may join up with another cow or with one or more subadults.

Male dominance relations

Dominance relationships may be evident either from differences in the behavioral actions displayed in encounters, or from patterns of avoidance. They may be expressed within a spatial context, as in territoriality, or be dependent upon individual identity independently of location. Where dominance is most strongly established, overt aggression may be rare. An initial contest may be needed to establish relative dominance, but in many cases it is assessed on the basis of auditory, olfactory or visual displays advertizing potential fighting ability.

Elephants

Asian elephant bulls exhibit periods of heightened sexual and aggressive activity, termed musth. Musth is associated with a copious secretion from temporal glands, and by continual dribbling of small amounts of smelly urine. Bulls in musth rub the temporal gland secretion on trees, and wander from one herd to another inspecting females for signs of estrus. A bull in musth manifests dominance over all other bulls in his vicinity, and non-musth bulls give way without contest. Bulls tend to show non-overlapping musth periods, so that it is rare for two males to be in musth in the same area. When this happens, one male either moves away, or comes out of musth. Musth periods generally last 2–3 months, and usually recur once annually, most often during the rainy season (Eisenberg, McKay & Jainudeen 1971; Jainudeen, McKay & Eisenberg 1972; Kurt 1974).

African elephant bulls exhibit a similar condition, revealed by a green exudate from the penis. However, temporal gland secretions are not restricted to males in musth, being shown by adult females at times. Scent marking of the environment has not been recorded, although twigs are sometimes inserted into the temporal gland orifice. Bulls in musth wander widely, and readily displace equally large bulls that are not in musth. It is rare for two bulls in the same area to be in musth at the same time. Mature males over 35 years of age typically show one musth period lasting 2–3 months each year. Among bulls that are not in musth a dominance ranking is evident. A more dominant animal holds his head higher, with ears out but relaxed, and may sniff the end of the trunk or the temporal region of the other bull. A subordinate bull places its trunk in the mouth or under the chin of the dominant bull. Several males not in musth may gather in the vicinity of a female in estrus, and fights may break out among them (Moss 1983; Poole & Moss, 1981).

Hippopotamus

Among hippos up to six adult or subadult males may share the same pool, but one bull is clearly dominant. Other bulls remain around the periphery of the pool, and when challenged demonstrate their submission by defecating with tail wagging in front of the dominant bull. Dominant bulls have lower testis testosterone levels than subordinate bulls, although there is no difference in sperm production.

Some pools or sections of lakeshore may be occupied by solitary hippo bulls without females, or by all-male groups. Since no more than one dominant bull occupies the same pool or region of lakeshore, these areas in effect represent exclusive territories. Neighboring dominant bulls meeting at a boundary stare, then present their rear ends and defecate, scattering their dung with their tails before returning to their own territories. Violent fights may break out when one dominantly behaving bull intrudes into another's territory, and lethal injuries can be inflicted with the lower canine tusks. However, males moving on land at night tend to ignore one another, and there is some overlap in the use of particular foraging areas. Both dominant and subordinate males scatter their dung with tail wagging movements, and commonly also urinate at particular sites alongside trails (H. Klingel personal communication; Laws 1984; Verheyen 1954).

Giraffe

Dominant bull giraffe demonstrate their status by standing tall upon encountering another bull. Young bulls engage in ritualized contests, striking one another with swinging blows of the head. A superior male may attempt to mount the other male at the end of the contest. This may serve to establish relative dominance without the need for a fight. No spatial exclusion among males in evident. Dominant bulls spend much of their time patrolling their home range core areas, reinforcing their dominance over males encountered, and investigating females. Fighting, involving powerful blows with the head, may develop when a strange male is encountered in an area (Pellew 1984a).

Rhinoceroses

Among Indian rhinos dominant males perform squirt-urination and foot-dragging displays. They are commonly found associated with females, but never with one another, although home ranges overlap. Males occupying adjoining home ranges rarely interact aggressively. However, violent fights, sometimes with fatal results, develop when strange squirt-urinating males intrude into an area. Submissive males do not squirt-urinate, with rare exceptions. They share the ranges of dominant males, and are sometimes tolerated close to the latter, while on other occasions they are chased. Some of the submissive males are young adults, while others are old individuals. Subadult males are also sometimes attacked and killed. Dung is deposited in piles bordering trails and feeding areas. Both dominant and subordinate males as well as females add to these accumulations, and the dung is not scattered (Laurie 1982; Ullrich 1964).

Sumatran rhino males commonly urinate in a spray directed over a bush, and may couple this with backwards scraping of the hindlegs and horning of the bush. Dominance relationships remain unknown. Both Sumatran rhinos and Javan rhinos accumulate their dung at particular sites (Borner 1979; Schenkel & Schenkel-Hulliger 1969b).

Black rhino bulls at Hluhluwe in Zululand occupy mutually exclusive territories, with one documented case of an apparently subordinate bull sharing a territory. A fight between two bulls was observed to take place at the boundary between their adjoining territories. In Namibia black rhino bulls occupy mutually exclusive home ranges, although other manifestations of territoriality have not been recorded. In East Africa male home ranges are much larger than observed in Zululand and overlap extensively. Bulls meeting one another respond in a variety of ways. Sometimes they stare at one another, but decline to meet. Sometimes a 'complex bull ceremony' takes place, involving stiff-legged scraping, 'imposing' postures, and charges. In some meetings the resident bull emits 'screaming groans', while the intruder is silent. Dominance rankings are thus not evident; but behavioral observations in East Africa have probably not been sufficiently intensive to discern them, considering the possibility that dominant and subordinate bulls may share the same home areas.

Black rhino bulls commonly eject their urine in a spray without any preceding actions. On other occasions they horn the ground, drag the feet (sometimes for distances of up to 10 m), and spray-urinate. Black rhinos commonly defecate on dung-heaps, and both sexes scatter their droppings with backwardly directed kicks (Goddard 1967; P. M. Hitchins personal communication; Joubert & Eloff 1971; G. Owen-Smith personal communication; Schenkel & Schenkel-Hulliger 1969a)

White rhinoceros

White rhino bulls occupy nonoverlapping home ranges, which are appropriately termed territories (Owen-Smith 1972 and 1975). Bulls leave their territories only to proceed to and from water, apart from occasional exploratory sallies. These territories covered areas of between 0.75 and 2.6 km^2, and were thus considerably smaller than the home ranges covered by white rhino cows. In the Kyle Game Park in Zimbabwe, somewhat larger territories were recorded, varying between 5 km^2 to 11 km^2 in extent (Condy 1973). A single adult male introduced into the Murchison Falls Park in Uganda moved over an annual range of 30 km^2, although he restricted his movements to an area of 6 km^2 during the wet season (van Gyseghem 1984).

In some instances two, or even three, white rhino bulls shared the same home territory, but in these cases one bull was clearly dominant and the other subordinate. Subordinate bulls stood with ears back giving loud roars when confronted by the dominant bull (Fig. 7.4). Most such confrontations were brief, lasting less than a minute, and ended when the dominant bull moved away. Dominant bulls ejected their urine in powerful sprays, while subordinate bulls and cows urinated in a conventional stream. Spray-urination was commonly preceded by a ritualized wiping of the anterior horn over a low bush or the ground, followed by scraping the legs over the site. Dominant bulls scattered their dung after defecating, while subordinate bulls only occasionally made a few ineffectual kicking movements. Females and subadults did not scatter their dung. Subordinate bulls sharing

Fig. 7.4 A white rhino subordinate bull stands giving the snarl display when approached by the resident territorial bull. From Owen-Smith 1975.

the same home territory appeared neutral in their relations with one another.

If two dominant bulls occupying adjoining territories met at a common border, they engaged in a ritualized confrontation (Fig. 7.5). The animals stared silently horn against horn, then backed away to wipe the anterior horn on the ground. These actions were repeated for periods varying from a few minutes to over an hour. Eventually the two bulls moved apart back into their own home areas. A dominant bull intruding into a neighbor's territory, generally on his way to or from water, displayed the same actions, but backed away steadily during the course of the confrontation, until he reached the border of his own territory.

Dominant bulls crossing more distant territories behaved like subordinate bulls. A wandering bull did not spray-urinate while outside his own territory, although he still scattered his dung. If accosted by another bull, the intruder stood with ears back making loud roars and shrieks. Generally such confrontations were brief, with the resident territory occupant moving

Fig. 7.5 Two white rhino territory holders stare horn against horn during a territory border confrontation. From Owen-Smith 1975.

off allowing the intruder to continue on his journey. However, some encounters with intruding bulls were more prolonged, and led to attacks or even fights. Subadult males in pairs were generally confronted briefly, while solitary subadult males were subjected to prolonged confrontations and sometimes attacked.

Dominant bulls spent more time engaged in 'other activities' than subordinate bulls, cows or subadults (Table 7.1). Part of this time was taken up by social interactions (mainly with females), and the remainder by walking, related to the patrolling of territory boundaries. Spray-urination sites were most densely concentrated along border regions between adjoining territories, and also along trails frequently used by rhinos. Dungheaps in border regions showed a characteristic central hollow, resulting from repeated visits by one or other of the neighboring territory holders every couple of days. Subordinate bulls spent more of their time standing looking around than did rhinos of other social classes.

Eleven instances of changes in dominance status were observed during my study. In three cases a strange bull moved into the study area displacing

Table 7.1. *Relative apportionment of time among 'other activities', by different social categories of white rhino*

Upper figure = percent of 'other activity' time. Lower figure (bracketed) = percent of total daily activity.

Age/sex class	Walking	Standing alert	Wallowing + rubbing	Drinking	Social interactions	Total	*N* days	*N* mins
Territorial bull	53 (9.7)	17½ (3.2)	8 (1.4)	3½ (0.6)	18 (3.3)	100 (18.2)	43	3174
Subordinate bull	47½ (6.5)	44 (6.0)	2 (0.3)	3 (0.4)	3½ (0.5)	100 (13.7)	14	851
Cow	42 (5.4)	20 (2.6)	12 (1.6)	3½ (0.5)	22 (2.8)	100 (12.9)	34	2503
Subadult	48½ (5.8)	20 (2.4)	25 (3.0)	4 (0.5)	2 (0.2)	100 (11.9)	20	1239

one of the resident bulls. In three cases previously subordinate bulls assumed dominance in a nearby territory (though never in the territory that they had occupied while a subordinate). One chain displacement occurred: a bull displaced by a newcomer remained in his home territory as a subordinate for three months, then assumed dominance in a territory 2 km away. The bull that he displaced remained one week, then took over dominance from an ageing male in the adjoining territory. The latter bull was still present as a subordinate in the same territory at the conclusion of my study 15 months later. Another deposed dominant bull shifted to the neighboring territory where he assumed subordinate status. One subadult male moved into the study area and took up residence as a subordinate bull.

In some cases a serious fight clinched the change in relative status between the bulls concerned, but in other instances the two bulls showed no more than minor gashes after the transition. Newly instated dominant bulls immediately set about placing their spray-urination marks all over the territory. Deposed bulls behaved like subordinate males: they ceased spray-urinating, stopped scattering their dung, and stood defensively with roars when confronted by the new territorial dominant. The latter treated them like any other subordinate bull, and did not drive them out of the area.

Summary

Male dominance relations are organized territorially in white rhinos, hippos, and in at least some populations of black rhinos. Elephants of both species and giraffes show a rank dominance system. Elephants furthermore show a temporally restricted period of heightened aggressive and sexual behavior. Indian rhinos show no spatial exclusion, but males appear tolerant of neighbours while strangers are likely to be attacked.

Courtship and mating

There are changes in female behavior and physiology associated with estrus. These elicit courtship responses from males, leading to copulation. Matings and resulting births may vary in the degree to which they are restricted seasonally. Prior dominance relations may govern mate access by males more or less strictly. Females can exert some choice over the sire of their offspring by avoiding less acceptable suitors.

Elephants

Among African elephants most conceptions occur during the rainy season. In the Luangwa Valley in Zambia, 77% of estimated conception dates fell during the 4 month period January–April. In the Kruger Park in

South Africa, 70% of conception dates occurred during the 6 wet season months of November–April. In the Hwange and Gonarezhou Parks in Zimbabwe, 88% of conception dates fell during November–April, except in one year with an extended rainy season when conceptions continued through May–June. Following a gestation period of 22 months, the birth peak usually occurs over October–December at the beginning of the wet season. In Uganda, where there is a bimodal rainfall distribution, there are two peaks in conceptions. At Amboseli in Kenya, which is on the equator, there is no strong seasonal pattern in reproductive activity (Hanks 1969b; Laws, Parker & Johnstone 1970; Sherry 1975; Smuts 1975c; Western & Lindsay 1984).

However, all of the above estimates of conception times incorporate an error in the ageing of small fetuses, causing these to be assigned birth dates about two months too late. The result is an underestimation of the degree of seasonality in births. Using a corrected formula, it was found that 93% of conception dates for elephants culled in the Chirisa and Chizarira Game Reserves in Zimbabwe fell during the rainy season months of November–April, with no conceptions occuring during the dry season months of June–August. The peak birth months in this area were December–February (Craig 1984).

During the wet season African elephant bulls roam widely, contacting and checking any females encountered. Searching behavior is not restricted to bulls in musth. However, searching may be largely a feature of low density populations where female units are dispersed. In other populations family units aggregate into large herds in the wet season, and may have a number of adult males associated with them. At Amboseli large males older than 35 years spent less time with female groups than younger males did, and were usually in musth when associated with a female group. Large dominant males tend to have their musth periods during the late wet season, with less dominant males coming into musth during the dry season.

Females in the early stages of estrus behave in such a way as to draw attention to themselves. Large numbers of bulls gather in the vicinity of such females – 10 on average at Amboseli, with a maximum of 67 recorded. The female actively remains close to a large musth bull if one is present. Other bulls keep their distance from the musth bull, but approach and pursue the female if the large bull moves away. Females try to avoid such overtures from younger males, and her companions may assist by attracting the attention of larger bulls with loud noises if she is caught and mounted by a medium-sized bull. Copulations are brief, lasting only 40 s on average. Estrus persists for 2–6 days, during which time a female may be mounted by several different males (Barnes, 1982b; Martin 1978; Moss 1983; Short 1966; Western & Lindsay 1984).

Asian elephant bulls wander from one female herd to another while in musth. Mating is not restricted to musth bulls. However, since bulls in musth are able to dominate other bulls, they monopolize matings when present. It is not uncommon for females to be mated by several different males in succession. Mountings last about half a minute, but intromission persists for only 8 s. In Sri Lanka there is a tendency for most births to occur over August–October, the transition period between the dry season and the start of the wet season, but the pattern varies somewhat between years (Eisenberg, McKay & Jainudeen 1971; Kurt 1974; Santiapillai, Chambers & Ishwaran 1984).

Hippopotamus

Among hippos in the Kruger Park in South Africa, 70% of births occur during the wet season months of October–March, with a peak in January–February. Since the gestation period is 8 months, the peak conception period is May–June in the early dry season. In Uganda conception peaks occur in February and August towards the end of each dry season, with corresponding birth peaks in October and April during the early rains (Laws & Clough 1966; Smuts & Whyte 1981).

Dominant hippo bulls periodically investigate the females clustered in their pools. An estrous female is pursued until she turns round and the pair clash jaws. This leads to a pushing contest until the female lies down in the water allowing the male to mount. Peripheral males keep away. Copulations are lengthy (Kingdon 1979; Verheyen 1954).

Giraffe

Among giraffe in the Timbavati Reserve in South Africa, 60% of conceptions occur during the late wet season months of December–March. With a gestation period of 15 months, the peak in births falls over March–July in the early dry season. In the Nairobi Park in Kenya, there is likewise a birth peak during the dry season, the peak months being August–September. However, in the Serengeti in Tanzania 45% of births occur over May–August, thus extending from the later part of the rainy season into the beginning of the dry season, and there is a lesser birth peak in December–January at the end of the short rains (Foster & Dagg 1972; Hall-Martin, Skinner & Van Dyk 1975; Pellew 1983a).

Dominant giraffe bulls investigate all female groups encountered, sampling the urine of each female in turn to test for estrus status. If no female is in heat, the bull departs. If the bull locates a female in estrus, he follows her, displacing any other male in attendance. The consort period lasts up to 3 days. A female may actively avoid the advances of other males. Fights between bulls can develop in the presence of an estrous female, but generally a dominant bull is able to displace other males simply by walking towards them. Copulations are brief. The dominant bull mates with most of the cows that come into estrus within his home range core area (Kingdon 1979; B. M. Leuthold 1979; Pellew 1984a).

Rhinoceroses

Indian rhinos at Chitwan in Nepal show a weak peak in the number of females in estrus over January–June, spanning the late winter and pre-monsoon period. Most births occur in July–August during the monsoon. The gestation period is 16 months (Laurie 1978).

Indian rhinos form pre-mating consort associations lasting a few days. Prolonged chases over distances exceeding 800 m are sometimes a feature of courtship. During these chases females make loud honking noises, while the male makes squeak-pants. Both sexes urinate frequently. These sounds and smells may serve to attract other males. The male remains with the female for a day or two after mating. Three dominant bulls occupying overlapping ranges at Chitwan each consorted with cows on different occasions, but submissive bulls were rarely seen with females. Matings average 60 min in duration under zoo conditions, and apparently endure for similar periods in the wild. Estrus recurs at intervals of 36–58 days if mating is unsuccessful (Lang 1961, 1967; Laurie 1978, 1982; Ripley 1952).

At Hluhluwe 65% of black rhino matings take place over October–December during the early wet season. Birth peaks occur in January–February (19% of observed cases) and over June–August (41% of observed cases). Allowing for a gestation period of 15 months, the latter period indicates a second peak in conceptions over March–May. In East Africa no seasonal variations in reproduction are evident (Hitchins & Anderson 1983; Goddard 1967).

Black rhino bulls remain in attendance for a period of 6–7 days prior to mating. Estrus lasts one day only. At Hluhluwe females may be mated several times; but in East Africa a single mating is the rule, although multiple mountings may occur. However, in East Africa there are cases of females being mounted by two or three different bulls in succession, while at Hluhluwe generally only a single bull is present. Attacks by the female on the male are sometimes a feature of courtship. Copulation durations vary between 20 min and 43 min. Intervals between successive estrus periods

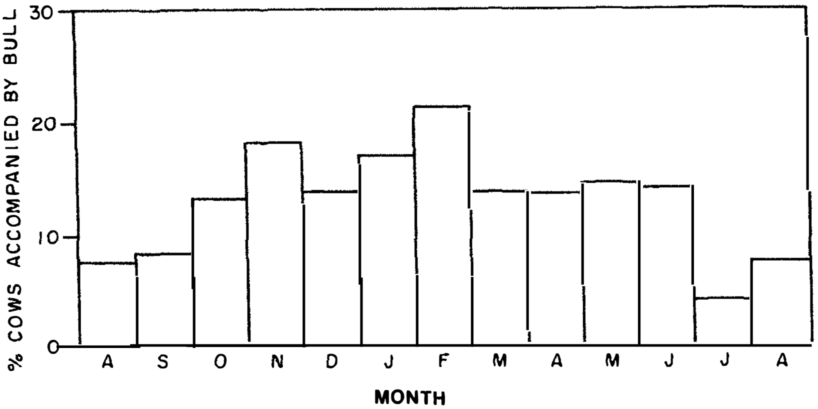


Fig. 7.6 Monthly variations in the proportion of white rhino cows being accompanied by bulls at Umfolozi (1968–71).

average 35 days (range 28–46 days) (Goddard 1966; Guggisberg 1966; Hitchins & Anderson 1983).

White rhinoceros

Among white rhinos the proportion of cows being accompanied by bulls (an indication of estrus) remains high through the wet season and early dry season months, dropping thereafter to low levels. Peaks are evident in November and in February (Fig. 7.6). Most of the associations between cows and bulls during the dry season are transient.

My records from Umfolozi indicated a gestation period of 16 months (based on the interval between the last occurrence of estrus, as revealed by an accompanying bull, and the birth date of the subsequent calf, from its estimated age when first seen). More exact estimates are available from captive animals: gestation periods of 484 days were recorded in the Krugersdorp Game Park in South Africa (Schaurte 1969) and 476 days in the Pretorius Kop enclosure in the Kruger Park in South Africa (M. C. Mostert personal communication). Zoo records show a modal gestation period of 490–500 days (Lindemann 1982).

Correspondingly calving peaks at Umfolozi occurred in March and in July (Fig. 7.7). The bimodal pattern could have been influenced by the midsummer droughts that occurred during the study period. Detailed observations show that the number of cows being accompanied by bulls tended to rise 2–4 weeks after good falls of rain, sufficient to induce a flush of green grass. Conversely, few cows were associated with bulls during dry periods. In the Kyle Game Park in Zimbabwe a similar bimodal pattern in births is evident, with peaks in April and in July (Condy 1973).

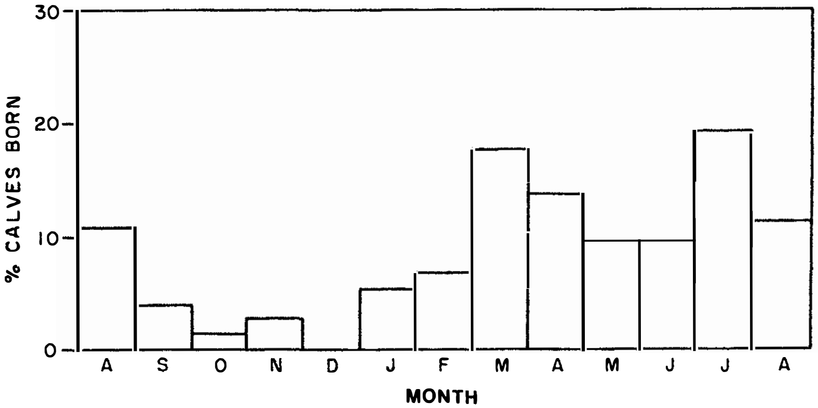


Fig. 7.7 Monthly variations in white rhino births at Umfolozi over 1968–71. (N = 74 calves).

Dominant white rhino bulls investigated cows encountered within their territories, while cows responded with threatening snorts or roars. Usually bulls moved away after perhaps a minute. If a bull remained with a cow for more than a day, this was a sign that the cow was coming into estrus.

During the pre-estrus consort period, the bull followed behind the cow and her companions. However, if the cow neared a territory boundary, the bull moved in front squealing to block her progress (Fig. 7.8). A confrontation sometimes ensued, with roars from the cow and squeals from the bull, occasionally lasting several hours before the cow turned back. Neighboring territorial bulls did not interfere, even though the sounds of such boundary blocking interactions were clearly audible over some distance. However, if a cow was able to evade the bull and cross into the next territory, the bull did not follow and she was joined by the neighboring bull.

The pre-estrus consort period typically lasted 1–2 weeks (Table 7.2). The onset of estrus was indicated by the commencement of repeated approaches by the bull, accompanied by a hic-throbbing sound. Initially the cow chased the bull away with a snort or roar. Eventually the cow tolerated the bull resting his chin on her rump. Several mounts usually occurred before intromission was achieved. The time interval between the first hic-throbbing advances and mating was about 24 hours. Copulations lasted 15–28 mins, with ejaculations repeated every few minutes. In one case a second copulation was observed after a bull had been forced off the cow by an overhanging branch at his first attempt (Fig. 7.9), but in other cases bulls made no further advances after a successful mating. However zoo records show instances in which two or three copulations occurred over 2–3 consecutive days (Lindemann 1982).

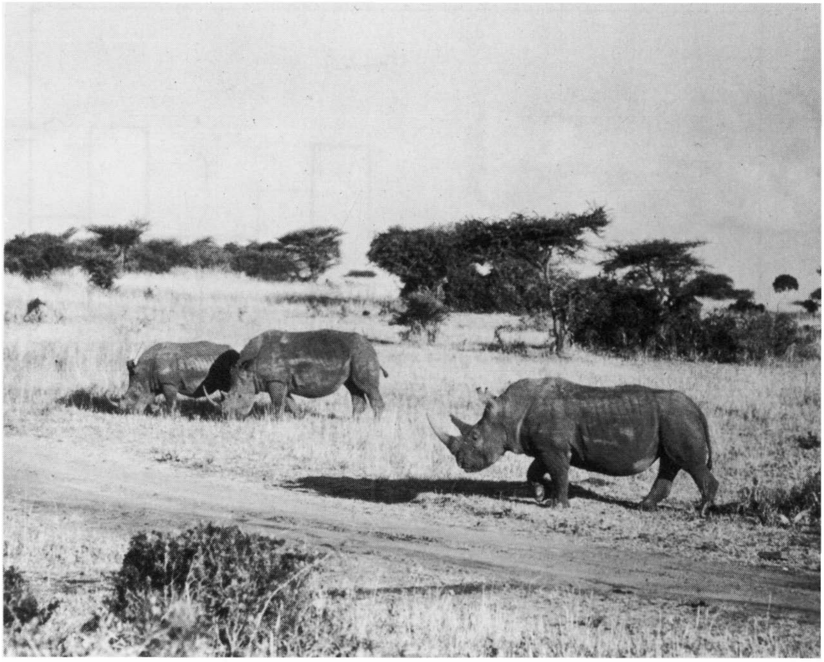


Fig. 7.8 A white rhino territorial bull moves round to block a cow and calf nearing a territory boundary.

Bulls usually remained associated with cows for 2–6 days after mating. Estrus recurred about 30 days later if mating was unsuccessful, but was not manifested if dry conditions prevailed. Zoo records show an estrous cycle period of 27–44 days, with estrus lasting 1–3 days (Lindemann 1982).

Subordinate bulls sharing the territory sometimes remained near a courting pair, but did not interfere. One case was observed in which a subordinate bull (who had been the dominant bull in the adjoining territory a year previously) attached himself to a cow and accompanied her for two days, at a time when the dominant bull in the territory was consorting with another cow. However the dominant bull then displaced him and courted and mated with this cow, while the subordinate bull circled around the pair displaying great agitation. After completing copulation, the dominant bull clashed horns briefly with the subordinate bull, then wandered off. The subordinate bull then attempted to court the cow, but was warded off vigorously.

One mating by a subordinate bull was observed, in unusual circumstances. There was no preceding consort period, and the dominant bull in the area showed no interest in the cow until the following month. The

Table 7.2. *Data on estrus and mating behavior by white rhinos*

	Mean	Range	*N*
Duration of consort period (days)			
(a) Pre-estrus	13	0–20	8
(b) Post-estrus	4	0–6	10
(c) Total	15	1–30	9
Duration of courtship (hours)	20	17–25	6
Number of mountings before copulation	3	1–7	6
Duration of copulation (mins)			
(a) Mounted	26	23–30	5
(b) Intromission	22	15–28	5

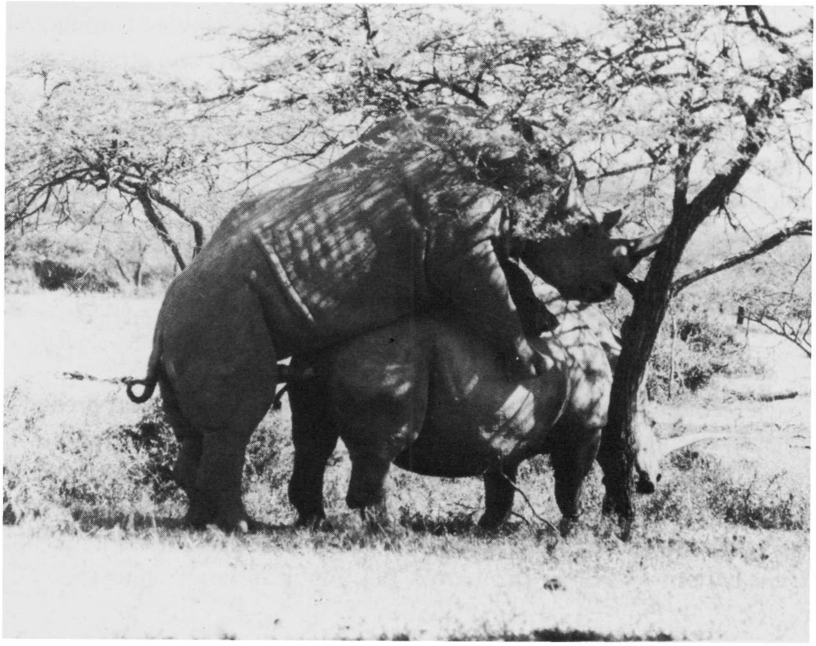


Fig. 7.9 A copulating white rhino bull being gradually forced off the cow by an overhanging branch.

copulation took place in an area that had formed part of the home area of the subordinate bull, but which had three weeks previously been incorporated into the neighboring territory following its takeover by a new bull. The subordinate bull did not remain with the cow after mating. Two and a half months later this subordinate bull moved away to assume dominance in a small territory elsewhere.

Summary

Among white rhinos, hippos, elephants and giraffes mate access is governed largely by prior dominance relations established among males. Among African elephants subdominant (i.e. non-musth) males may contest matings in the absence of a large dominant bull. Among black rhinos and Indian rhinos the relation between prior dominance and mating remains unclear. Chases, fights or loud vocalizations, which may serve to attract other males to the scene and thus allow some degree of mate choice to be exerted, are shown by elephants and the various rhino species. Copulations are prolonged in rhinos and hippos, brief in elephants and giraffes. Post-mating guarding is evident in white rhinos and hippos. Gestation lasts over a year in all species except hippo. Seasonal variations in reproduction are evident in all species. In elephants, white rhino, black rhino and giraffe, conception peaks occur during the wet season, while in Indian rhino and hippo mating peaks fall within the dry season. Birth peaks fall during the dry season in white rhino, black rhino and giraffe, while in elephants the birth peak occurs in the early part of the rainy season.

Responses to predators

Animals may respond to the threat posed by potential predators either by fleeing, attacking or standing defensively. Alarm displays may be given to draw the attention of companions to the threat, or to signal to the predator that it has been detected. Of special interest are the actions of mothers to protect their vulnerable offspring. Potential predators include not only lions and other carnivores, but importantly also humans.

Elephants

African elephants have no audible alarm call, and the cessation of the low growling rumbles exchanged among group companions supposedly signals a threat. The recent discovery that elephants make low frequency sounds below the range of human hearing (Payne, Langbauer & Thomas 1986) may change this interpretation. Members of family units bunch tightly together at threatened danger, whether from lions or humans, with

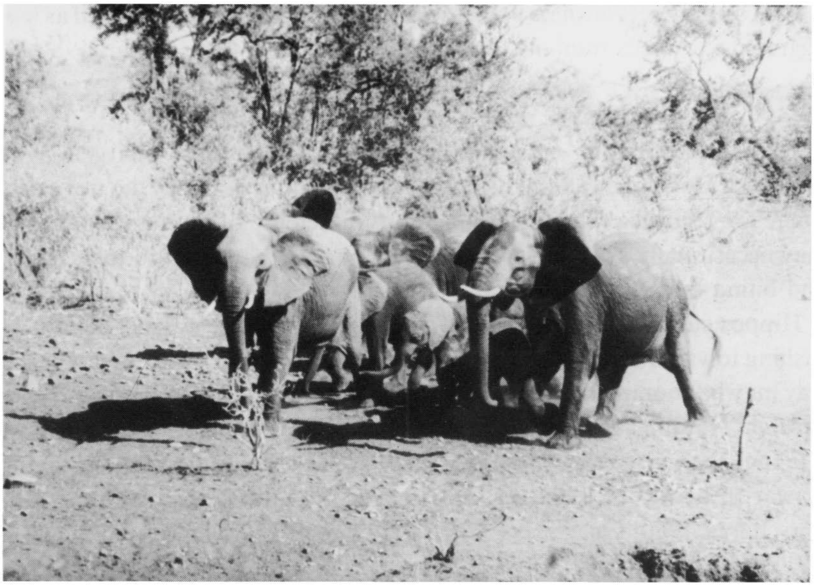


Fig. 7.10 A family unit of African elephants bunches together when threatened by a nearby vehicle.

young animals in the center (Fig. 7.10). Family units approaching water chase aside any lions encountered. Adult males take little notice of lions (Kingdon 1979).

For human observers the risk of following family units is much greater than that of following elephant bulls. This is due not only to the problem of avoiding a greater number of animals, but also because cows more often display aggression on detecting a nearby person than do bulls. However, most commonly family members bunch together and make off in haste. In the Kruger Park in South Africa, attacks on vehicles are most often by adult females, and commonly occur when a car drives between a mother and her calf. I was once chased in a vehicle over a distance of about one kilometer by a family group of elephants, the matriarch in the group leading the charge. At Lake Manyara in Tanzania, a family group of elephants made a sudden and silent coordinated attack, involving three females, on a vehicle parked close by. Bulls commonly demonstrate at a threatening person or vehicle by flapping their ears, trumpeting and making advancing rushes. Fatal attacks by both bulls and cows on humans are not uncommon where humans on foot frequently contact elephants (Barnes 1979; Douglas-Hamilton 1972; Guy 1976a; personal observations).

Asian elephants used to convey tourists in the Kaziranga Sanctuary in

Assam display nervousness in the vicinity of tigers. They are regarded as less aggressive towards humans than African elephants (Eltringham 1982).

Hippopotamus

Adult hippos encountering lions on land may charge open-mouthed. However, at night hippos amble past lions as if they did not exist. There are records of females killing lions in defense of their young. Lions may occasionally kill fully-grown hippos by rolling them onto their backs and biting the chest and throat.

Hippos surprised on land by humans generally take evasive action by rushing towards water along the nearest path. However, any human in the way may be chomped by the huge jaws with potentially fatal results. In the Virunga National Park in Zaire, hippos are responsible for more human fatalities than any other large mammal. Hippos feeding on land at night appear to be less of a danger. Alarm calls are undescribed (Bourliere & Verschuren 1960; Guggisberg 1961; Kingdon 1979; Schaller 1972).

Giraffe

Adult giraffe may stand watching lions from ranges as close as 20 m, but run off if the lions appear to be stalking. In one recorded instance a giraffe reared up and slashed at an attacking lioness with both forelegs, before fleeing. Giraffe mothers may successfully defend their calves against lions, standing over the calf directing powerful kicks at any approaching lion. Giraffe are inoffensive so far as humans are concerned. Giraffe have no audible alarm call (Pellew 1974a; Schaller 1972).

Rhinoceroses

Indian rhino mothers generally run off behind their calves when alarmed. When disturbed by humans, Indian rhinos sometimes respond by rushing towards the intruder making snorting sounds, although usually they can be turned aside by shouts. Mothers with small infants frequently charge. Fatal attacks on local villagers occur, injuries being inflicted with the lower incisor tusks. Indian rhinos give a snort when disturbed by the sounds of an approaching animal, including another rhino (Laurie 1978; Ullrich 1964).

Adult black rhinos commonly pay little attention to lions. At waterholes they may advance on lions forcing the latter to give way. In one incident at Ngorongoro in Tanzania, a subadult male lion attacked and pursued an 11 month old black rhino calf, separating it from its mother. The mother followed, and when the lion diverted its attack to her, she killed it with several horn thrusts. Hyenas have been observed attempting to pull down calves up to 4 months in age by grabbing them from behind. In these incidents the mother charged the hyenas when the attacked calf squealed, forcing them to retreat. Black rhino calves generally walk behind the mother; but when disturbed the calf may flee in front of the mother for the first 50–100 m, after which the mother takes the lead (Goddard 1967; Schenkel & Schenkel-Hulliger 1969a).

Black rhinos are renowned for their aggressive charges both towards vehicles, and humans on foot. Many of their advances are merely curious approaches, the animal wheeling and making off once the human is clearly identified. Others seem to be directed charges, accompanied by steam-engine-like puffs, especially if an animal is suddenly disturbed at close quarters. Attacking blows are struck with the horn if the person or vehicle is contacted, but if evasive action is taken the animal continues on its way. At Tsavo in Kenya black rhinos commonly reacted to human scent with a rapid advance over a distance of 5–20 m, then turned and made off. However, if human scent was combined with visual or auditory stimuli, their responses were less predictable. Often they reacted with immediate flight. On occasions inquisitive approaches and short rushes occurred. Black rhinos in a group sometimes stopped in a fan formation, after having fled for a distance. In one incident a black rhino bull charged from 40–50 m range upon detecting a human silhouette visible against the skyline (having been alerted by oxpeckers). The animal chased the person around a tree, and inflicted a horn wound when the person fell out of the tree. The rhino then ran off. In the Ngulia area of Kenya where black rhinos had been hunted from early times by people armed with poison arrows, rhinos were extremely truculent and ready to charge instantly (Guggisberg 1966; Ritchie 1963; Schenkel & Schenkel-Hulliger 1969a).

White rhinoceros

I observed four encounters between white rhinos and lions, which had recently colonized the western section of Umfolozi where the study area was situated. In one instance an adult male white rhino lay down to sleep while the lions settled 30 m away. In another case a white rhino cow with a year-old calf ignored a group of four young lions that lay watching 15–20 m away, while the lions made no move to attack. At a waterhole a group of seven lions was present while numerous white rhinos moved past to drink. One cow accompanied by a subadult advanced towards the lions, which bounded out of her way at 12 m range. Another cow with a two-year-old calf stood peering at two lions lying about 5 m in front of her. The lions made no

Fig. 7.11 A white rhino calf runs off in front of its mother.

attempt to stalk the white rhinos, though they advanced towards an approaching group of zebra.

White rhino cows with newborn infants did not charge even when I approached quite close. They displayed great agitation, but remained standing over the calf. If alarmed by detection of a human intruder, a cow immediately rushed beside her infant with loud pants, and *vice versa.* The pair then ran off, the calf galloping in front of the mother (Fig. 7.11). The horns of white rhino cows tend to be longer and more slender than those of bulls, and in some females the horns project forwards rather than upwards from the snout (Fig. 7.12), a condition not recorded among males. Female horns thus seem more effectively designed for warding off attacking carnivores, while the stouter horns of males are better able to resist horn-to-horn blows during intraspecific combat.

At distances of up to 800 m, white rhinos responded to human scent by standing peering about uneasily. At closer ranges their immediate response was to flee, usually downwind. If the breeze eddied, they shuffled about agitatedly facing in different directions, until able to detect an auditory or visual clue, then they ran off. In one incident, a white rhino subadult that

Fig. 7.12 A white rhino cow with a forward-pointing horn.

had detected signs of my presence had difficulty in communicating its alarm to its group companions. It shuffled about agitatedly making intention movements towards running, but as the other rhinos detected nothing they resumed feeding. The panting sounds made by white rhinos are not alarm calls, but serve as contact sounds in a variety of contexts.

Red-billed oxpeckers (*Buphagus erythrorynchus*) generally reacted to a nearby human by giving loud churring calls. This caused the rhinos they were sitting on to react by looking around apprehensively. If the birds continued calling, the rhinos shuffled around nervously searching for a sign of the cause of the birds' alarm. At any slight noise or movement, the rhinos immediately ran off.

White rhinos were unable to identify me visually as a human intruder at ranges greater than 20–30 m, provided that I remained immobile. On occasions they appeared confused and uncertain how to respond, shuffling around agitatedly, perhaps starting to run off, but then standing their ground again. Approached on foot from a vehicle near one of the tourist roads, white rhinos were less likely to run off than elsewhere in Umfolozi, provided that the approach was made openly in full view. Under these

Fig. 7.13 A group of four white rhinos stands in a defensive rump-against-rump formation.

conditions a group of white rhinos commonly adopted a rump-to-rump formation, standing facing outwards in different directions (Fig. 7.13).

Occasionally white rhinos rushed towards me when alarmed, but they were usually turned aside by noises. However, on two occasions I experienced a directed charge. In the one instance a white rhino bull suddenly charged when I stepped aside from the bush behind which I had been standing at 5 m range. When I slipped on wet grass the rhino dodged me, but tossed my assistant to one side with its head while he was trying to run away. In another case a white rhino bull accompanying a cow suddenly charged when I clicked my camera from 5 m range, but turned aside at a few meters range when I shouted. Steele (1968) describes an incident in which he was chased by a white rhino bull over some distance, and eluded it only by diving into an antbear hole. There is a record of a woman being killed by a white rhino just outside Umfolozi Game Reserve. In the Sudan Lang (1920) experienced only one charge while hunting white rhinos, and that was from an animal that had been wounded.

Summary

Adult megaherbivores generally respond indifferently or aggressively towards lions and other predators. Carnivores attempting to catch young animals may be killed by defending mothers. Responses towards humans vary between fleeing and attacking, depending on circumstances. White rhinos and giraffes are generally inoffensive, while elephants, Indian rhinos, black rhinos and hippos are quite commonly aggressive. Alarm calls are lacking in all species, except possibly elephants.

Comparisons with smaller ungulates

Small species of antelope are either solitary or occur in small loose groups; while females plus young of larger species form stable herds typically numbering 10 to 30 or more animals. African buffalo occur in large herds of 100–2000 animals including adults of both sexes. In their lack of sociality rhinos, and to a lesser degree hippo and giraffe, resemble small bovids. Elephants differ from other species in the hierarchical structure of their groupings. Female–young units occupying discrete home ranges have been identified in impala, and may occur among other antelope species (Jarman 1974; Leuthold 1977a; Murray 1982b; Owen-Smith 1977).

In most African ungulates male dominance relations are organized in the form of the spatially restricted dominance of territoriality. Exceptions include species forming large mixed-sex herds like African buffalo; semi-nomadic species like plains zebra; and browsing antelope species such as kudu. White rhino and hippo, and in some areas black rhino, conform to the territorial dominance pattern; while giraffe resemble other browsers in their loose rank dominance system. Elephants are unique in having the temporally restricted dominance of musth superimposed on a rank dominance pattern. Satellite males sharing territories, as occur in white rhino, hippo and perhaps black rhino, are found also in waterbuck and Grevy's zebra (Owen-Smith 1977).

Most ungulate species have narrowly restricted breeding seasons, with birth peaks occurring during the wet season when food availability is optimal. Breeding is less seasonally concentrated in certain species occupying equatorial regions. A few ungulates, for example waterbuck, roan antelope and African buffalo, show a fairly broad birth peak, like that typical of megaherbivores, even in southern Africa. The longest gestation periods among African bovids and equids are 12 months, in the case of zebra, and 11 months in the case of African buffalo; while all megaherbivores except hippo have gestation periods exceeding one year.

All medium-sized ungulate species have alarm calls, and in some cases also visual displays, which they give on detecting a nearby predator. These lead to coordinated flight if the predator is within attack range. Megaherbivores lack specific alarm signals; while small antelope like grey duiker have sniffing calls that they give while running off from a disturbance. All bovids and equids flee from human intruders, except for African buffalo bulls. Megaherbivores flee only from humans, and may on occasions attack humans as well as threatening carnivores. Among bovids where females possess horns, the horns of females tend to be designed as stabbing weapons, while male horns are stouter at the base and so better able to resist the forces of horn-to-horn combat (Packer 1983). A similar pattern is manifested by the two African rhino species, though not among other megaherbivores.

8

Life history

Introduction

As animals grow and age they pass through different functional stages in terms of their social relations and contribution to reproduction. These stages may be subdivided as follows (i) infancy and juvenilehood – the period of complete or partial dependence on the mother for sustenance and protection; (ii) adolescence and subadulthood – the early period of independence from the mother, through attainment of physiological sexual maturity; (iii) adulthood – the period following attainment of full social and sexual maturity. Interest lies in the timing of these stages, and in the changing behavioral patterns of animals as they pass through each stage.

Infancy and juvenilehood

This period commences with birth. During the early neonatal period the offspring is completely dependent upon its mother for sustenance in the form of milk. During later infancy the offspring starts supplementing its milk intake with vegetation, but it is some time before nursing ceases and weaning is complete. By use of the term infancy I imply the period during which the young animal could not survive if separated from its mother. Juvenilehood refers to the period of partial dependency on the mother for perhaps some food supplementation, or at least protection from predation. In most species the juvenile period ends when the young animal is driven away by the mother around the time of birth of the next progeny. However, in some species older offspring may remain associated with the mother and her companions through adolescence.

Elephants

African elephant cows give birth in the company of their group companions. Other females in the group gather around the newborn infant, the matriarch assisting the mother in removing the fetal membranes. A newborn elephant is able to stand, although unsteadily, about 20 min after birth, and nurses for the first time about 30 min after being born. About an hour after birth it is able to follow its mother and her companions, although requiring some assistance (Leuthold & Leuthold 1975).

African elephant calves begin feeding on vegetation at 3 months of age, and by 24 months spend a similar proportion of their time feeding to adults. Calves under 24 months in age do not survive if orphaned. Suckling takes place frequently, on average every 37 min for male calves and every 50 min for female calves. The mean duration of suckling bouts is about 90 s for both sexes. Nursing generally continues until the birth of the next offspring, i.e. typically for about 4–5 years. In a few instances calves stopped suckling after 4 years of age despite a longer interval to the birth of the next offspring, while a small proportion of calves continue suckling after the birth alongside the younger sibling. The oldest recorded age at weaning is 8 years. Instances of females nursing calves that are not their own offspring are rare.

Juvenile elephants spend most of their time within less than 5 m of their mothers (median distance 2 m) until 8 years of age (Fig. 8.1). Calves seek one another out and engage in much challenging, wrestling and mutual pushing play while the family is resting or drinking. Juvenile and adolescent females comfort, assist and protect calves in their family units which are not necessarily their siblings (Douglas-Hamilton 1972; Lee & Moss 1986; Lee 1987; Sikes 1971).

Hippopotamus

Hippo females move to a secluded area on the river or lakeshore, or to shallow water, to give birth. The neonate remains in the exclusive company of its mother for the first few days after birth. The young nurse under water. Some hippo groups contain fewer calves than lactating females, suggesting that calves may nurse from more than one female. Infants commence feeding on grass between 6 and 8 weeks of age. Under captive conditions calves continue nursing until about 14 months old (Laws & Clough 1966; Smuts & Whyte 1981; Verheyen 1954).

Giraffe

Giraffe mothers return to specific areas to give birth in seclusion. The newborn infant remains isolated from other giraffes for 1–3 weeks, with the mother returning to suckle it 2–4 times per day (night behavior is unrecorded). Infants start nibbling on plants at 2 weeks of age. For the first 3–4 months calves spend most of their time lying out alone, or in the company of other young giraffes. Mothers move as far as 3 km away from

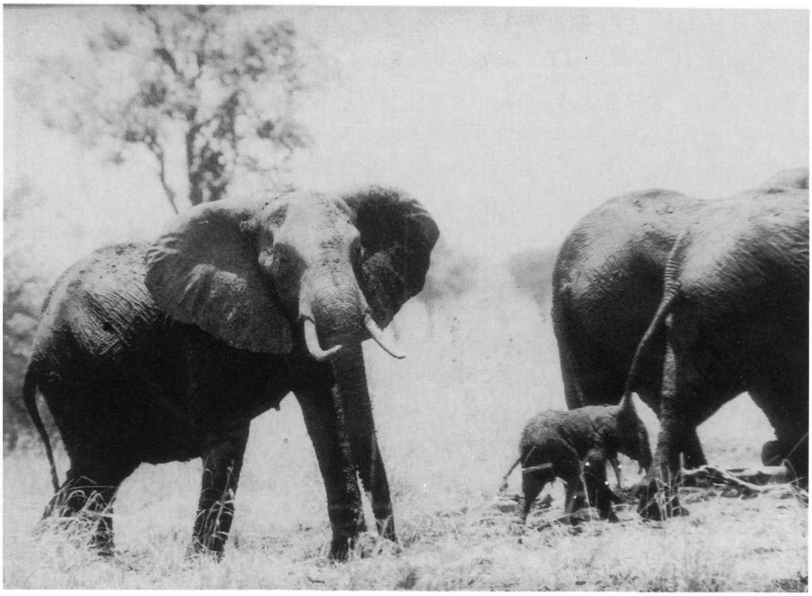


Fig. 8.1 African elephant infant close behind its mother.

their offspring. Sometimes calf pools are formed, including one or two adult females in the company of several small calves. Juveniles nurse 2–3 times during daylight hours, for about a minute at a time. Male calves initiate 70% of their nursing bouts, but female calves only 50%. Youngsters may attempt to nurse from females besides their mothers, but are rarely successful. Calves engage in playful running and jumping, especially when in groups. By five months of age young giraffe move with a group for part of the day, and feed for more than half the day. By 6–9 months the activities of the calf are similar to those of its mother. Cows continue lactating for 12–13 months. Young giraffe drift away from their mothers between 12 and 18 months of age (Hall-Martin, Skinner & Smith 1977; Langman 1977; Leuthold & Leuthold 1978; B. M. Leuthold 1979; Pratt & Anderson 1979; Pellew 1984a).

Rhinoceroses

Indian rhino females seek seclusion in thick grassland or forest to give birth, and are particularly aggressive towards other rhinos while the calf is young. Up to 6 months of age the offspring may be left lying alone for periods of over an hour while the mother forages up to 800 m away. Calves aged up to one year nurse four or more times during daylight, older calves

Fig. 8.2 White rhino cow standing over her day-old calf in thick bush.

once or twice daily. Nursing bouts typically last 3–4 min, with suckling continuing until calves are about two years old. Young calves inquisitively approach other rhinos to engage in nasonasal nuzzling, which sometimes develops into playful sparring; but older calves tend to respond aggressively when approached by another rhino. Juveniles are driven away by the mother a week or more before the birth of the next offspring. In some cases periodic reunions between the older calf and its mother occur over the first few months following separation, especially if the offspring is a male (Laurie 1978).

Black rhino cows may leave a newborn infant hidden for the first week following birth. Nursing bouts last about four minutes, but frequency of nursing has not been documented. Infants start nibbling on bushes when only a few weeks old. Calves generally keep within 25 m or less of their mothers, except during locomotory play. Mothers separated from their calves make breathing calls. Suckling may continue until the calf is as old as 19 months. Youngsters become independent of their mother around the time of the birth of the next offspring, when aged about 2.2–3.3 years. In some situations the older offspring rejoins its mother after the birth of the

Table 8.1. *Frequency and duration of nursing by white rhino calves*

		Nursing frequency		Duration of nursing		
Age range (months)	Total no. of records	Mean per hour	h. of observ.	Mean	(min) Range	*N*
0–2	14	1/ 1.0	13	3.5	1.0–6.0	12
2–6	5	1/ 2.3	7	2.9	2.3–3.5	3
6–12	30	1/ 2.4	38	2.9	1.3–5.0	16
12–18	43	1/ 4.8	97	3.6	2.8–7.0	18
18–24	5	1/15.0	30	3.8	—	1

new calf (Frame & Goddard 1970; Hall-Martin & Penzhorn 1977; Schenkel & Schenkel-Hulliger 1969a).

White rhinoceros

I encountered white rhino females with newborn infants either in patches of dense thicket (Fig. 8.2), or in one case on a hillslope secluded from other rhinos. Mothers favored densely wooded areas until calves were about two months old. Infants less than two months old nursed hourly, while older calves nursed at intervals of about 2.5 hours. Nursing bouts typically lasted about three minutes (Table 8.1). Suckling frequency declined between 12 and 18 months of age, but one 24 month old calf was recorded still being suckled. It seems that cows ceased lactating in their third or fourth month of pregnancy, so that suckling continued longer if the birth interval was prolonged.

Infants started nibbling at grass at about 2 months, but not until they were over a year old did they spend as much time feeding as the mother (Table 8.2). Mother and offspring kept close together, generally within half a body length (2 m) of one another, with separation distances tending to increase with increasing age (Table 8.3). Cows that had lost their calves wandered around making repeated panting calls, while a calf separated from its mother made high-pitched squeaks.

Infant calves engaged in locomotory play, running back and forth over distances of 5–15 m at a stretch. Calves displayed great curiosity upon encountering other rhinos, and commonly approached to sniff. Meetings between calves frequently led to playful chasing and head to head tussles. White rhino calves remained associated with their mothers until the time of the birth of the next offspring. The older calf was then persistently driven away by the mother. Only in rare cases did older calves rejoin their mothers.

Table 8.2. *Proportionate time spent grazing by white rhino calves relative to the mother at different ages*

Activities recorded at 5 minute intervals during observations sessions.

Age range (months)	No. of records with cow grazing	No. of records calf also grazing	% time spent gr. rel. to cow
0–2	19	0	0
2–4	52	14	27
4–8	43	27	63
8–12	41	37	90
12–24	44	44	100

Table 8.3. *Separation distances from the mother maintained by white rhino calves of different ages*

	Separation distances (m)						
	Mean	Range	Distribution (%)				
Age of calf			0–4	5–9	10–19	20+	*N*
<2 months	1.4	0–15	100	0	0	0	21
2–4 months	2.5	0–15	83	13	4	0	52
4–12 months	2.2	0–15	91	7	2	0	84
12–24 months	3.7	0–25	81	11	4	4	47

Summary

Rhino and hippo calves are left lying out for a period of up to a week, while giraffe calves remain lying out for several months. Elephant calves move with their mothers' family units from the day of birth. In all species calves nurse several times daily, and mothers continue suckling for a year or longer. Despite the solitary habits of rhinos, social play is a feature of all species. Rhino mothers drive away the older offspring when the next calf is born, while young giraffe drift away of their own accord. Elephant and hippo females tolerate continuing associations by older offspring.

Adolescence and puberty

Following severance of the mother–offspring bond, immature animals may either wander alone or attach themselves to other companions. The onset of puberty is indicated by the beginning of spermatogenesis in males, and by the occurrence of the first ovulatory cycles in females. However, full fertility may not be attained until some time later. Males do not achieve social maturity until they have attained mature weight, and thus become able to compete successfully with older males. Females attain adult status following the birth of their first calves. I use the term adolescence for the prepubertal period following independence from the mother. The term subadult is applied generally to the complete period from breaking of the mother–offspring bond to attainment of social maturity.

Elephants

Young African elephants of both sexes remain with their maternal family units after weaning. Females typically undergo their first ovulation between 11 and 14 years of age. The earliest recorded age at first conception is 7 years, while under conditions of malnutrition ovulation may be retarded until as late as 20 years of age. The mean age at first parturition varies between 13 and 18 years in different populations, with a minimum age of 8 years recorded. Growth by females levels off between 15 and 20 years (Douglas–Hamilton 1972; Hanks 1972a; Jachmann 1986; Lang 1980; Laws 1969b; Laws, Parker & Johnstone 1975; Lee & Moss 1986; Sherry 1975; Smuts 1975c).

Male African elephants begin spermatogenesis between 7 and 15 years of age, but full sperm production is not reached until 10–17 years. Males leave family units between 10 and 16 years of age, in some cases in response to aggressive behavior by the adult females. They then join up with other males of similar age and older. The first musth periods start at about this time. Males seem to show a growth surge in height and weight between 20 and 30 years of age, although measurements of hindfoot length failed to confirm this. Males do not attain full weight and hence competitive ability until 30–35 years of age (Douglas–Hamilton 1972; Hanks 1973; Laws, Parker & Johnstone 1975; Lee & Moss 1986; Moss 1983; Sherry 1975).

The above ages were generally estimated using Laws' (1966) dental ageing criteria. However, there is evidence that this method may overestimate true ages by 2–4 years in the age range 10–25 years. If this is confirmed, some quoted ages might need to be revised accordingly (Croze, Hillman & Lang 1981; Jachmann 1985; Lang 1980; Lark 1984).

Asian elephant females may reach sexual maturity between 7 and 8 years of age, and produce their first calves at 9–10 years. Males tend to become peripheral to their maternal units at 6 years, suggesting that puberty is reached between 7 and 10 years. Musth periods usually commence around 19–20 years, but some males do not show musth until 30 years of age. Subadult males become semi-nomadic, remaining in an area for several days then disappearing (Eisenberg, McKay & Jainudeen 1971; Jainudeen, McKay & Eisenberg 1972; Kurt 1974; McKay 1973).

Hippopotamus

The age of first ovulation among hippo females varies between extremes of 3 and 20 years, with about 9–11 years most typical in wild populations. Zoo records indicate ages at first parturition between 3 and 8.5 years. Males first start producing sperm at 2 years of age, with peak sperm production occurring by 6 years. A captive male was sexually potent at 3.2 years. However, asymptotic weight is only reached at 25–30 years of age, and dominant bulls are generally aged at least 26 years. Young females tend to remain associated with their maternal group (Dittrich 1976; Laws 1968a; Sayer & Rahka 1974; Skinner, Scorer & Millar 1975; Smuts & Whyte 1981).

Giraffe

Female giraffe show a mean age at first conception of 4–5 years, with a minimum of 3.8 years in the wild. Captive giraffe females attain puberty at a mean age of 3.9 years, with the earliest record being 2.8 years. Males become sexually potent at about 3.5 years, but do not reach full weight and hence social maturity until aged 8 years or more. Subadult male giraffe wander widely (Hall-Martin & Skinner 1978; Pellew 1984a).

Rhinoceroses

In Indian rhinos, adolescent males tend to join other young males, while adolescent females usually attach themselves to adult females. However such associations generally last only a few days. Adolescents in groups are less likely to be attacked by adult males than lone adolescent males. Adolescent females sometimes remain in the maternal home range, while adolescent males tend to move out of high density areas. At Chitwan, females produce their first offspring between 6 and 8 years of age. In zoos, females achieve sexual maturity as early as 3 years of age, while males became sexually potent at 7 years (Lang 1967; Laurie 1978).

Black rhino adolescents sometimes join up with other adolescents or with cows, but the majority are solitary. Some subadults wander widely. Nasonasal contacts occur when adolescents encounter other subadults or cows, and playful horn sparring may develop between subadults (Goddard 1967; Schenkel & Schenkel-Hulliger 1969a).

In East Africa, black rhino females first mate at an age of 4.5 years, with first parturition occurring at about 6 years of age. At Hluhluwe, the earliest recorded matings occurred at 7–8 years of age, but earliest parturition did not occur until 12 years. In the adjoining Umfolozi-Corridor region, there were two records of females giving birth at ages of 6.5 years and 8.5 years respectively. Black rhinos introduced from Kenya into the Addo Park in the Cape showed a mean age at first parturition of 6.3 years (after the initial unsettled period), with a minimum of 5.1 years. Among black rhinos held in zoos, the mean age at first conception is 6.4 years, with a minimum of 5.0 years. Males at Hluhluwe do not commence spermatogenesis until 8 years of age, but a captive male reportedly sired a calf at an age of 3.5 years. There is suggestive evidence that one male mated at 6 years of age at Addo. Males do not become territorial until at least 9 years old at Hluhluwe (Goddard 1967; Hall-Martin & Penzhorn 1977; Hall-Martin 1986; Hitchins & Anderson 1983; Lindemann 1982).

White rhinoceros

White rhino adolescents became separated from their mothers when aged between 2 and 3.5 years. Thereafter they wandered about attaching themselves temporarily to cows or to other adolescents, until after a month or two a more stable bond was formed. In the Umfolozi study area two-thirds of adolescents joined other adolescents, while one third formed a persistent attachment with a cow lacking a calf. However, the proportion of subadults joining cows may have been atypically high, due to the number of cows that had had their calves removed by the rhino capture team operating on the periphery of the study area. Cows without calves readily accepted several subadults as companions. Only two cases were recorded in which a calf rejoined its mother and her new offspring.

In some instances particular pairs of adolescents remained together for periods of several years (Table 8.4). Bonds were formed equally readily with a companion of the same or opposite sex. However, bonds formed between pairs of young males tended to last longer than those involving females, because of the delayed maturity of males relative to females. Attachments with cows were of limited duration, since the subadult companion was driven away when the cow produced her next calf.

While some subadult pairs or trios were resident in the study area, other subadults appeared to be semi-nomadic. New individuals appeared in the study area, were seen there several times over the course of a few days, then disappeared again. Two subadult females marked with eartags in the study area were subsequently seen 15 km and 25 km away respectively.

Subadults of all ages displayed great interest in meeting other rhinos. Nearly half of their encounters with other subadults, and one third of their encounters with cows, led to nasonasal contacts (Fig. 8.3). Forty percent of such contacts developed into playful horn sparring engagements.

Solitary tendencies started to develop in some young males at an age of

Table 8.4. *Social nature and duration of stable bonds formed by white rhino subadults*

A bond enduring one month or longer is regarded as stable.

Age/sex categories	No. of stable bonds recorded	Av. min. bond duration[a] (months)	Max. recorded duration (months)
A. Subadult pairs			
(i) Male–male:			
Adolescents < 6 yrs	6	8.7	20.5
Subadults > 6 yrs	7	13.6	26
All ages combined	13	11.3	
(ii) Female–female:			
Adolescents < 6 yrs	7	3.7	9.5
Subadults > 6 yrs	7	3.7	5
All ages combined	14	3.7	
(iii) Male–female:			
Adolescents < 6 yrs	8	4.1	15.5
Subadults > 6 yrs	5	4.2	8.5
All ages combined	13	4.2	
B. Cow–subadult pairs			
(i) Cow–subadult male:			
Adolescent < 6 yrs	7	7.4	22
Subadult > 6 yrs	1	21	21
All ages combined	8	8.1	
(ii) Cow–subadult female:			
Adolescent < 6 yrs	10	10.2	26
Subadult > 6 yrs	2	11.2	12
All ages combined	12	10.3	

Note: [a] The period between first and last sightings of the same two individuals still together.

about 8 years, while other males remained associated with a subadult companion until 11–12 years. One young male was monitored regularly through the transition period from subadulthood to subordinate bull status. Between the ages of 8 and 9 years, he attached himself temporarily to various cows or subadults, being associated with such companions in 54% of sightings ($N = 37$). Over the succeeding year, he was with other rhinos on only 7.5% of days seen ($N = 92$). Between the ages of 10 and 11 years, he was essentially solitary, being associated with other rhinos in only 3.5% of sightings ($N = 83$).

At Umfolozi, the three youngest females evidently in estrus, as judged by hic-throbbing advances by an accompanying male, were aged 3.8 ± 0.2 years, about 4.0 years, and about 4.5 years, respectively. The youngest age at first parturition was 6.5 ± 0.5 years. Three other females were estimated

Fig. 8.3 Nasonasal meeting between two white rhino subadults.

to be about 7 years of age (± 1 year) when they produced their first offspring. Among zoo-kept animals, the mean age at first parturition is 5.6 years (range 5.1–6.2 years) for known-age animals, and about 8 years for animals for which only the year of birth was known (Lindemann 1982).

Young females remained attached to their companions, including in some cases similar-aged young males, through their first estrus periods. Subadult male companions displayed no sexual interest, and were not driven away by the courting bull. Around the time of parturition females separated themselves from their group associates, and did not rejoin them. Their behavior patterns were thereafter similar to those of adult females.

Subadult males aged up to 8–9 years generally showed no indication of sexual interest in females. However at Hluhluwe North, in the absence of a dominant bull, three young males aged 8–10 years made repeated hic-throbbing advances towards a subadult female, but did not proceed beyond the chin-on-rump posture. The youngest dominant territory holder in the Umfolozi study area was estimated to be about 12 years old. One territorial bull in the Kyle Game Park in Zimbabwe was known to be 12.5 years old (Condy 1973).

In the Pretorius Kop enclosure in the Kruger Park in South Africa, there is a record of a young male siring his first offspring at an age of 7.9 years, incidentally mating with his mother. No mature bull was present (M. C. Mostert personal communication). From zoos it is reported that one male sired a calf when aged 5.5 years (Lindemann 1982).

Summary

In elephants and hippos adolescents remain associated with their natal groups, while in rhinos adolescents of both sexes are driven away by the mother when she next calves. Females attain puberty at 2–3 years in giraffe, 4–7 years among rhinos, and 7–14 years among elephants. Puberty among males generally occurs 1–4 years later than it does in females. Young elephant males leave their maternal groups at puberty. Males of all species do not attain full weight and hence social maturity until well after puberty. Captive animals may attain maturity younger than wild animals. Hippos appear especially variable in the ages at puberty of both males and females.

Reproduction by females

Females remain reproductively active throughout the adult period. Features of interest are the intervals between successive births, changes in fertility with age, and the sex ratio of the offspring produced.

Elephants

For African elephants mean conception intervals vary between 3.3 and 5.5 years in various regions, including Lake Manyara in Tanzania, Luangwa Valley in Zambia, Kruger Park in South Africa, Gonarezhou and Hwange in Zimbabwe, and Tsavo and Amboseli in Kenya. The shortest mean interval is that for the Luangwa Valley population prior to 1968. These are long-term means based on the relationship between the number of placental scars and the age of the female, determined from culled samples.

Short term natality rates, estimated from the ratio of pregnant to nonpregnant females, show a wider variability, due to year to year variations in the proportion of females conceiving. In the Murchison Falls Park in Uganda, the mean birth interval was estimated to be 9.1 years for the population north of the Nile River, and 5.6 years for the population to the south of this river, based on shot samples spanning 1–2 years during the 1960s. However, samples obtained from the same regions over 1973/74, following population reduction, indicate a mean birth interval of 5.1 years for the northern population and 3.6 years for the southern one. An analysis of placental scars in the same samples yielded a mean birth interval of 4.9 years for the Murchison Falls Park South population; while a mean calving interval of 3.8 years was estimated based on animals killed in this region over the period 1947–51. At Tsavo in Kenya, a mean birth interval of 6–7 years was estimated from the ratio of pregnant to nonpregnant females just prior to major starvation mortality during a drought. At Amboseli in Kenya, individually recorded birth intervals averaged 5.6 years during a series of dry years, and 3.5 years over a subsequent sequence of wet years. At Kasungu in Malawi, the mean birth interval between surviving calves was 3.3 years. The shortest birth interval for a female in the wild where the previous calf survived at least one year is 2.8 years (Douglas-Hamilton 1972; Hanks 1972; Jachmann 1986; Laws 1969a; Laws, Parker & Johnstone 1970, 1975; Lee & Moss 1986; Malpas 1978, cited by Croze *et al.* 1981; Moss 1983; Perry 1953; Sherry 1975; Smith & Buss 1973; Smuts 1975c; Williamson 1976).

The proportion of African elephant females pregnant is highest (43%) in the age group 31–40 years. Fertility declines rapidly after 50 years of age. Fetal sex ratios for African elephants vary from 111 males : 100 females in the Kruger Park ($N = 298$) to 95 males : 100 females ($N = 188$) in Gonarezhou in Zimbabwe. In the combined data from all sources, the primary (fetal) sex ratio is 102 males : 100 females ($N = 710$) (Hanks 1972; Sherry 1975; Smuts 1975; Williamson 1976).

Birth intervals of Asian elephant females are about 4 years both in the wild and in captivity. A minimum birth interval of 23 months was recorded following the death of a calf, but the shortest interval after a surviving calf is 36 months (Kurt 1974).

Hippopotamus

Hippo females typically show mean calving intervals of about 2 years. However, in the Kruger Park in South Africa only 5.6% of females were pregnant during a severe drought, compared with 37% in other years. In Uganda about 15% of females examined were reproductively inactive, i.e. neither pregnant nor lactating. Fetal sex ratios show equal proportions of males and females (96 males : 100 females, $N = 269$). Females show little indication of reproductive senesence (Laws & Clough 1966; Smuts & Whyte 1981).

Giraffe

Giraffe exhibit a mean calving interval of 20 months in wild populations, with a range between different areas of 16 to 25 months. For captive animals the mean birth interval is 21.5 months (range 15.6–40 months). However the modal birth interval from all sources is 16–18 months. In the Nairobi Park in Kenya, the birth interval averaged 17 months when the calf died shortly after birth, but 23 months when it survived. The secondary (i.e. birth) sex ratio of giraffe generally shows an excess of males. The sex ratio of calves born in zoos is 160 males : 100 females (N = 115). Wild populations at Tsavo and Nairobi in Kenya yielded a juvenile sex ratio of 159 males : 100 females (N = 467) (Bourliere 1961; Foster & Dagg 1972; Hall-Martin 1975; Hall-Martin & Skinner 1978; Leuthold & Leuthold 1978; Pellew 1983a).

Rhinoceroses

Indian rhinos at Chitwan in Nepal show a median calving interval of 2.8 years. A female that had her newborn infant killed by a tiger calved again after an interval of 18 months. Two aged-looking females did not give birth over a four year period, while the third produced a calf, but lost it within 6 weeks. One female estimated (from cementum lines in her tusks) to be about 30 years old was not pregnant when she died, despite a 3 year interval since her last calf. The sex ratio of calves sighted on more than five occasions was 18 males : 16 females (Laurie 1978).

Black rhinos at Tsavo in Kenya show a mean calving interval of about 2.5 years; while at Ngorongoro and Olduvai in Tanzania, and Amboseli in Kenya, the mean birth interval is about 4 years, including females that did not produce a calf during the observation period. The shortest observed calving interval is 25 months. Black rhinos at Hluhluwe exhibit a mean birth interval of 2.7 years, and those in the adjoining Corridor and Umfolozi a mean interval of 2.3 years, excluding females that did not appear with a calf over the 3.3 year observation period. Including the latter cases, the mean birth intervals become 3.9 years and 2.5 years respectively. The shortest observed calving interval was 20 months. Black rhinos introduced from East Africa into the Addo Park in South Africa show a mean calving interval of 32 months (excluding a few very long intervals), with a minimum of 27 months when the previous calf had survived and 24 months after the calf had died. The birth sex ratio at Hluhluwe is 146 males : 100 females (N = 86). At Tsavo the juvenile sex ratio is 129 males : 100 females (N = 119). Black rhinos born in zoos include 35 males and 39 females (Goddard 1967, 1970a; Hall-Martin & Penzhorn 1977; Hitchins & Anderson 1983; Klös & Frese 1981, reported in Lindemann 1982).

White rhinoceros

Birth intervals recorded for individually known white rhino cows in the main Umfolozi study area varied between 22 months and 3 years 5 months. The modal birth interval was 2.0–2.5 years (Fig. 8.4), and the mean

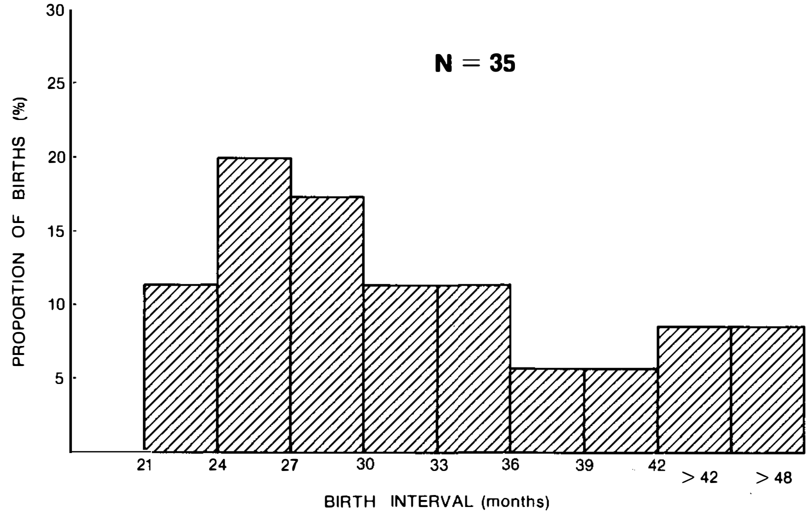


Fig. 8.4 Distribution of individual birth intervals of white rhino cows in the Madlozi study area.

2.6 years ($N = 32$, Table 8.5). Age-related differences in calving intervals were apparent. Three out of the four primaparous females in the sample exhibited calving intervals of less than 2.5 years; while 6 of the 8 cows that appeared elderly either had calving intervals exceeding 3 years, or failed to appear with a calf during the observation period of nearly 3 years.

Estimates of calving rates were also available from the proportion of females with young calves less than a year old in population samples from four different areas in Umfolozi in 1968. This ratio underestimates the calving rate to the extent that infant mortality had occurred. These data suggest that the calving rate was higher elsewhere in Umfolozi than in the main study area at Madlozi (Table 8.5). Based on all study areas combined, the mean natality rate was 0.40, equivalent to a mean calving interval of 2.5 years.

Data for white rhino populations introduced from Umfolozi into other wildlife parks show mean calving intervals varying between 2.7 and 3.5 years (Table 8.6). Zoo records indicate a mean birth interval of 24 months (range 17–44 months), but this includes cases where the previous calf died shortly after birth. Patterns vary among zoos, San Diego exhibiting a mean birth interval of 20 months ($N = 29$), compared with 29 months at Whipsnade ($N = 11$) and 28 months for all other zoos ($N = 21$). One individual cow at San Diego produced six calves in nine years at an average interval of 18.5 months (Lindemann 1982).

The birth sex ratio at Umfolozi was obtained from the sexes of all calves

Table 8.5. *Variation in natality rate among white rhino cows in different years and study areas*

Study area	Year	No. of cows observed	No. of calves born	Specific natality per Ad♀ per year
Madlozi	1968	42	13	0.31
Madlozi	1969	45	15	0.33
Madlozi	1970	43	13	0.30
Madlozi	1971	40	17	0.43
Madlozi	All years combined	(170)	58	0.34
Nqutsheni	1968	55	21	0.38
Gqoyini	1968	35	20	0.57
Dengezi	1968	28	10	0.36
All study areas	1968	160	64	0.40

Table 8.6. *Birth intervals and natal sex ratios recorded for different populations of white rhino*

Area	Period	N	Mean calving interval (y)	Sex ratio ♂:♀
Madlozi area, Umfolozi G.R.	1968–71	53	2.63	35:18
Pretorius Kop enclosure, Kruger Park	1965–78	19	2.70	12:7
Matopos Game Park, Zimbabwe	1967–77	23	2.85	9:14
Kyle Game Park, Zimbabwe	1967–75	23	3.45	7:16

Sources: Data for other areas supplied by M. C. Mostert, National Park Board of South Africa, for Pretorius Kop; and by J. H. Grobler and C. J. Lightfoot, Zimbabwe Department of National Parks, for Matopos and Kyle respectively.

born at Madlozi during my study, supplemented by the sexes of juveniles less than a year old seen elsewhere. Since juvenile mortality between birth and one year of age was less than 8%, the latter sample should deviate insignificantly from the sex ratio at birth. For the total sample the birth sex ratio was 173 males: 100 females, which is significantly different from parity (Table 8.7, $N = 139$, Chi square $= 4.7$, $P < 0.05$). A similar preponderance of males among subyearling calves was recorded by Hitchins during the 1972 helicopter census of the Umfolozi–Hluhluwe complex (26 males: 14 females), and by Brooks during a horseback survey of Umfolozi in 1974 (32 males: 21 females).

Table 8.7. *Sex ratio of white rhino calves born at Umfolozi in different years and regions*

	Year of birth				
Area	1968 ♂:♀	1969 ♂:♀	1970 ♂:♀	1971 ♂:♀	All years ♂:♀
Madlozi	8:5	11:4	9:4	7:5	35:18
Nqutsheni	14:7	4:1	2:1	0:1	20:10
Gqoyini	7:10	3:2	0:1	—	10:13
Dengezi	5:5	2:0	—	2:0	9:5
Hluhluwe North	1:0	0:1	—	—	1:1
Umfolozi west environs	4:2	2:0	—	—	6:2
Umfolozi south	—	—	7:2	—	7:2
Combined	39:29	22:8	18:8	9:6	88:51
			Overall ratio		173:100

Table 8.8. *Sex ratio of white rhino calves in relation to preceding calving interval*

	Area				
Preceding calving interval	Madlozi ♂:♀	Pretorius Kop ♂:♀	Matopos ♂:♀	Kyle ♂:♀	Combined ♂:♀
1.8–2.3 y	6:1	2:2	1:1	0:1	9:5
2.3–2.8 y	5:3	1:0	2:2	0:2	8:7
2.8–4.6 y	4:5	2:3	1:4	4:6	11:18

Sources: Acknowledgements as in Table 8.6.

The sex ratio of white rhinos born in zoos is 147 males : 100 females (N = 121, Lindemann 1982). Records from white rhino populations introduced from Umfolozi into other wildlife areas show that a preponderance of male calves is not a general feature. In the Pretorius Kop enclosure in the Kruger Park in South Africa more males than females were produced, but in the Kyle and Matopos Parks in Zimbabwe an excess of female calves was recorded (Table 8.6). If the natal sex ratio is analyzed in relation to the preceding birth interval, for all records combined, there is an apparent tendency for male calves to predominate after short birth intervals, and female calves after long ones (Table 8.8). However this tendency is not statistically significant, due to the small sample size. At Umfolozi younger females tended to give birth at shorter intervals than older ones. If the sexes of the calves born at Madlozi is related to the age category of the mother,

Table 8.9. *Sex ratio of white rhino calves in relation to age of the mother*
Based on calves recorded at Madlozi, 1966–71

Age of mother	No. of individuals Cows	 Calves	Sex ratio ♂:♀
Young cow, with first or second calf	7	11	9:2
Prime cows	28	51	32:19
Ageing cows	8	14	5:9
All cows combined	43	76	46:30

males predominate strongly among first and second-born offspring, while ageing cows gave birth mainly to daughters (Table 8.9).

One cow clearly of advanced age at Umfolozi had no calf with her in 1966 nor in 1968, but produced a calf in 1970. Another elderly cow was accompanied by a calf born in 1965 when first seen. In 1970 she had no calf with her, but was in estrus. Possibly she had given birth in 1968 or 1969, but had lost the calf. Four other elderly cows failed to appear with a calf over the total period of nearly four years spanned by records. Thus it seems that white rhino cows continue producing calves throughout their lifespan, but that with advancing age birth intervals lengthen while infant mortality increases.

Summary

Among megaherbivores, typical birth intervals vary from about 2 years in giraffe and hippo to about 4.5 years in elephants. Shortest birth intervals, where the preceding calf survived, are 16 months for giraffe and 2.8 years for elephants. Rhinoceroses are intermediate. In all species natality rates can vary widely between years and among different populations. White rhino, black rhino and giraffe show variable, but generally male-biased sex ratios at birth; while elephants and hippo produce equal proportions of males and females. There is clear evidence of reproductive senescence among female elephants, and suggestive evidence for female white rhinos and hippos.

Reproduction by males

Males vary in the period over which they are reproductively active during adulthood, as influenced by their ability to maintain dominant status in relation to other males. Males may not attain prime competitive ability until some time after puberty. With advancing age males decline in physical prowess, even though they may remain sexually potent.

Elephants

Among African elephants, musth seems to be restricted to bulls over 30 years in age, although younger bulls may mate if given an opportunity. At Amboseli in Kenya, the success rate of courtship chases by bulls increases with age, from 15% for young adult males aged 21–25 years to 30% for males aged 26–35 years, and 54% for males over 35 years. This was largely due to evasive action by females against younger males. As a result large bulls over 35 years perform 65% of all copulations, although they form only 12% of the population of sexually potent males (> 12 years). Bulls that appear notably aged, and are thus probably over about 50 years, spend little time with females (Hall-Martin 1984; Moss 1983; Poole & Moss 1981; Western & Lindsay 1984).

Most Asian elephant bulls have undergone musth by 30 years of age. The majority of males show musth once annually, but males in poor condition may not show musth for periods of up to 4 years (Jainudeen, McKay & Eisenberg 1972).

Hippopotamus

Hippo males do not achieve asymptotic testis weights until 26–30 years of age, and dominant herd bulls are generally over this age. However, some culled groups contained two males in this age class, suggesting that some prime-aged males hold subordinate status (Skinner, Scorer & Millar 1975; Smuts & Whyte 1981).

Giraffe

Giraffe bulls do not obtain mating opportunities until 8 or more years old. A relatively small number of high-ranking bulls perform most of the copulations. Old bulls show declining sexual activity.

Rhinoceroses

Among Indian rhinos, some males were frequently associated with females, while others were rarely with females (Laurie 1978). No information is available for black rhinos on differing statuses among adult males.

White rhinoceros

Among white rhinos, dominant territory holders consisted mostly of prime-aged males, while subordinate bulls sharing territories included a preponderance of either young adults or ageing animals (Table 8.10). Overall two-thirds of adult males were dominant territory holders, while

Table 8.10. *Comparative age distribution of white rhino territorial bulls and subordinate bulls*

	No. of individ. classif.	Young adults	Prime adults	Old adults
Territorial bulls	36	3	30	3
Subordinate bulls	23	7	7	9
Combined	59	10	37	12

one third were subordinates, but among prime-aged males 80% were territory holders. In the Madlozi study area bulls held dominant status in the same territory for a mean duration of 5.4 years, although elsewhere in Umfolozi territory changes appeared to occur somewhat less frequently. Most prime males claimed another territory after being deposed. Young or old bulls either dispersed to occupy territories in less contested regions, or became subordinate bulls in favorable territory locations.

Summary

In all megaherbivores males do not attain full weight and hence social maturity until several years after puberty. Prime-aged males dominate reproduction, but some prime males may be relegated temporarily to subordinate status. Old males become relegated to peripheral status.

Mortality and lifespan

The risk of mortality varies over the lifespan, being high during infancy and old age and low during the prime period of maturity. Males commonly incur higher mortality rates than females, part of which may derive from reproductive competition. Episodes of higher than average mortality occur during periods of severe drought and reduced food availability. Potential lifespans are difficult to record in the wild. However, ages may be estimated in culled specimens from patterns of tooth wear, and counts of cementum lines evident in sections of teeth. A limitation in the assignment of chronological ages is the availability of representatives of known age. Zoo records reveal upper limits to potential lifespans.

Elephants

For African elephants at Manyara in Tanzania, annual mortality averaged 10% during the first year of life, thereafter declining to 3–4%, but about half of this mortality was related to hunting. At Amboseli in Kenya, where there was no hunting, calf mortality totalled 7.5% between birth and one year of age, and 15% by 2.5 years, in wet years. During dry years there was a sex difference in calf mortality: first year mortality among males averaged 25% compared with 10% among females, while 55% of males had died by 2.5 years compared with 30% of females. Above 2.5 years, annual mortality rates drop to levels similar to those of adults. In Uganda, mortality among adult elephants was estimated to be 5–6% per annum, due mostly to shooting. At Tsavo in Kenya, annual mortality was 2–2.5% for prime females aged 15–40 years and for males up to 25 years of age; among older males mortality accelerated to 7.5% per annum, but probably incorporated past hunting. At Luangwa Valley in Zambia, the mean mortality rate of animals aged 10–50 years was 4.4% per annum. All of these estimates are based on the age structures found in shot samples, and thus assume a stationary population. They overestimate true mortality rate to the extent that these populations had been increasing rather than stationary (Douglas-Hamilton 1972; Hanks 1972; Laws 1969b, 1974; Laws, Parker & Johnstone 1975; Lee & Moss 1986).

Predation on calves by lions has been documented at Manyara in Tanzania and Kasungu in Malawi, but is probably more widespread. At Tsavo there is a record of a 7–8 year old elephant killed by lions (Douglas-Hamilton 1972; R. H. V. Bell personal communication).

Catastrophic elephant mortality occurred in the Tsavo East National Park in Kenya over 1970–71, when the rains failed over two consecutive years. At least 6000 elephants, or 15% of the total population of 40 000, died over this period. Most of this mortality was concentrated in the northern and central region of Tsavo East National Park, where rainfall remained under 200 mm per annum over two successive years. In this region mortality was estimated to be 70% for mature females, and even higher among dependent calves under 3 years. However, mortality among adult males was only 10% over these two years. Deaths were due to starvation following the elimination of most of the edible vegetation around remaining water sources. At Amboseli in Kenya, 76% of calves born in 1977 died during a severe drought. In the Ruaha Park in southern Tanzania, elephant mortality as indicated by found tusks was concentrated in the second half of the dry season, and increased in a drought year. Tusk sizes indicated that a higher proportion of young animals died during droughts than in other years (Barnes, 1982c; Corfield 1973; Moss, cited in Croze *et al.* 1981; Phillipson 1975).

However the elephant population in the Tsavo West Park, an area with a somewhat higher mean rainfall than that in Tsavo East, failed to show any notable increase in mortality during the 1970–71 drought. During the severe

1982–83 drought experienced in the Kruger Park in South Africa, the elephant population showed no decline, although calf proportions were subsequently low. The desert elephants occupying the Damaraland region of Namibia suffered no drought-related mortality at times when populations of smaller ungulates were decimated, but calf production suffered (G. Owen-Smith 1986 and personal communication; Phillipson 1975; Walker *et al.* 1987).

Life tables for African elephants show a steep rise in annual mortality after an estimated age of 50 years, associated with a decrease in the grinding area of the teeth. However, no captive African elephant has survived longer than about 44 years. For Asian elephants potential longevity in captivity is typically 50–60 years, with a maximum age of 67 years recorded. Hence it is estimated that African elephants in the wild have a potential lifespan of 55–60 years (Laws 1966).

Hippopotamus

For hippos in Uganda, mortality rates are estimated to be 45% between birth and one year, and 4% per annum thereafter. In the Virunga Park in Zaire, young hippos made up about 20% of recorded lion kills. They are also a significant prey of lions in the Kafue Park in Zambia, although elsewhere they generally form a negligible proportion of lion kills. The longevity record for a zoo-kept hippo is 49 years.

Hippos may suffer severe mortality during drought periods. In the Kruger Park in South Africa at least 170 hippos died during the 1970–71 drought. In the 1982–83 drought the population in the Levhuvu River in Kruger Park declined to 30% of its predrought level, with very few calves remaining in the surviving population (Bourliere & Verschuren 1960; Laws 1968b; Schaller 1972; Smuts & Whyte 1981).

Giraffe

For giraffe, calf mortality during the first year varies between 33% and 55%, with most losses occurring during the first month post-partum. Among adults, females experience an annual mortality of about 3–4%, and males about 8–9%, with young males being especially vulnerable. In the Central District of the Kruger Park, giraffe made up 11% of recorded lion kills, but due to their large size formed an estimated 43% of the food intake of lions. Based on the estimated total populations of lion and giraffe, the annual kill rate of giraffe amounts to perhaps 20% of the giraffe population. However, it is likely that giraffe are overestimated in kill records because of their large, conspicuous carcasses. In the Timbavati Reserve adjoining the Kruger Park, most giraffe kills occur during the late dry season, indicating malnutrition as a contributing factor. Giraffe appear to be more important as lion prey in South Africa than they are in East Africa. The highest recorded age for a captive giraffe is 28 years. There are records of both males and females exceeding 25 years in age in the wild (Foster & Dagg 1972; Hall-Martin 1975; Pellew 1983a; Schaller 1972; Smuts 1978, 1979).

Giraffe suffered little mortality either in the Kruger Park or in the adjoining Klaserie Reserve during the severe 1982–83 drought. However, in September 1981 a die-off of giraffe amounting to about half the population occurred in Klaserie, following an exceptionally cold spell. An important consequence of unusually severe cold in the South African lowveld is the frosting of evergreen tree foliage in bottomland areas, resulting in the loss of this critical food source (Walker *et al.* 1987).

Rhinoceroses

For Indian rhinos at Chitwan in Nepal, mortality rates were 3.4% per annum for adults (about one quarter of this due to poaching), 1.2% per annum for subadults, and 8.5% per annum for juveniles. Perinatal losses amounted to 5.6%. Predation by tigers was responsible for about half of the recorded calf mortality. Fighting accounted for nearly 30% of the deaths due to causes other than poaching. The greatest longevity recorded for an Indian rhino in a zoo is 47 years. The oldest animal recorded in the Chitwan population, based on counts of cementum lines in the teeth of animals found dead, was estimated to be about 30 years (Laurie 1978, 1982; Reynolds 1960).

Annual mortality rates of black rhinos at Hluhluwe were 3.5% for adult females, 7.3% for adult males, and 5.7% for immature animals. Neonate losses, incorporating barren females and prenatal mortality as well as postnatal deaths, amounted to 69% at Hluhluwe, but only 9% at Umfolozi. At Tsavo in Kenya, annual mortality rates average about 10% for prime-aged adults and 16% for calves, but these estimates based on found skulls assume a stable population. Black rhinos rarely feature in lion kill records, though there is an instance of a yearling killed and eaten by lions in the Serengeti. Hyena predation seems to be largely responsible for the poor survival of black rhino calves at Hluhluwe, and hyenas may be important predators on calves under 4 months old in East Africa. A black rhino female in the Chicago zoo reached an age of 49 years, before she was destroyed; while other records indicate zoo longevities of up to 38 years (Goddard 1970a; Hitchins & Anderson 1983; Lindemann 1982; Schaller 1972).

Table 8.11. *Mortality estimates based on histories of individually known white rhinos in the Madlozi study area in Umfolozi Game Reserve*

Age class	No. of dif. indiv.	Animal-years observed	No. dying	Mortality % p.a.
AD♂	25	54.8	2	3.6
AD♀	42	98.5	1	1.0
Calves	40	57.8	2	3.5

At Hluhluwe a die-off of about 15% of the black rhino population occurred in 1961, affecting all age classes. Some animals showed partial paralysis of the hindquarters before dying, suggesting the possibility of plant poisoning. Nearly 300 black rhinos died from starvation along a 64 km section of the Athi River in Tsavo National Park in Kenya in 1961, and several hundred more died during the 1970–71 drought in the same region. However, the black rhino population occupying the Namib desert region appeared resistant to droughts that affected other ungulate species (Goddard 1970a: Hitchins & Anderson 1983; G. Owen-Smith 1986).

White rhinoceros

I estimated mortality rates from the disappearance of known individuals from the study population, in relation to the total period over which animals of each age/sex category were monitored. Only five animals disappeared, presumed dead, over the 2.8 year study period, including two adult males, one adult female, and two calves aged 12 months and 18 months respectively. The resulting estimates of annual mortality are adult males 3.6%, adult females 1%, and calves 3.5% (Table 8.11). Only a proportion of the subadults in the study was individually recognizable, and none of these animals died. However, 3 unidentified subadults were found dead over the 3.3 year period. Since the mean number of subadults in the area was 15, this suggests a mortality rate among subadults of 6% per annum.

Perinatal mortality is difficult to detect, due to the secretive habits of cows with newborn calves. One calf was known to have disappeared between 2 and 7 days of age, but only because its mother was fitted with a radio transmitter. Indirect evidence of infant mortality is available from the calving histories of individual females. Documented calving intervals varied between just under 2 years and a little over 3.5 years. Thus if a cow did not produce a calf over a 4 year period, it could be presumed that she was either infertile, or had aborted during pregnancy, or had lost the calf shortly

Table 8.12. *White rhino deaths recorded in Umfolozi Game Reserve in Natal Parks Board files*

		Adults + Subadults			Juveniles			
Period	Years	♂	♀	Total	♂	♀	Total	Total
Aug 1962–Aug 1965	3	19	8	31	5	3	13	44
Aug 1965–June 1967	2	23	13	49	0	1	5	54
June 1967–July 1968	1	6	6	14	1	0	1	15
July 1968–Sept 1969	1	11	4	18	1	0	4	22
Oct 1969–Sept 1970	1	3	2	12	0	1	2	14
Sept 1970–Mar 1971	0.5	—	—	—	—	—	—	11
Total	8.5	62	33	124	7	5	25	160
%		54	29				17	

Sources: From Vincent 1969, and unpublished records.

after birth (the observation period was extended to four years by considering the age of the accompanying calf when each cow was first seen). Only three cows at Madlozi failed to appear with a new calf during this period; while 45 calves were born, 44 of which survived beyond one week of age. The effective calf loss is thus 4/48, or 8.3%. This represents the upper limit for neonate mortality, since it includes cases of infertility and prenatal losses as well as postnatal losses.

I also recorded the age classes of white rhinos found dead outside the study areas, and assigned found skulls to age classes. My records were supplemented by the records of white rhinos found dead reported in Natal Parks Board files. Of the adults plus subadults found dead, two thirds were male (Table 8.12). Juveniles are almost certainly underrepresented because of the rapid disappearance of their small carcasses and skulls. Some adult and subadult carcasses are probably also missed, despite the extensive coverage of the area by rangers, and the large numbers of vultures that congregate on white rhino remains. Arbitrarily it will be assumed that two-thirds of all adult and subadults deaths are recorded, yielding an estimated total of 25 adults plus subadults dying annually. Accepting the age and sex structure of the reconstructed 1969 population (Table 11.6), the following estimates of annual mortality were obtained: adult males 12, or 3.0%; adult females 6, or 1.2%; subadults 7, or 1.1%. These estimates are in close agreement with those calculated for the study population, except in the case of subadults.

Of the 16 cases in which cause of death could be established, 5 were related to injuries received during fighting. All 5 of these animals were males (three adult, two subadult). Six deaths were due to accidents such as falling over a cliff or becoming stuck in mud, two were possibly due to illness, and three could be related to senescence. Neither at Umfolozi nor Hluhluwe did white rhino calves show torn ears to indicate attacks by hyenas. A white rhino male was killed by lions in Umfolozi shortly after my departure (P. M. Hitchins, personal communication). From the Kruger Park in South Africa there are records of a white rhino calf killed by lions, and of a bull attacked and mauled so badly by lions that he had to be destroyed (Pienaar, 1970).

Low rainfall conditions occurred in Umfolozi over 1967–70, 1972–73, and even more severely through 1978–83. Increases in white rhino deaths recorded during these periods were relatively minor, amounting to no more than 50–100% above normal levels. Likewise, in the Kruger Park no increase in white rhino mortality was recorded during the 1982–83 drought. However, over 100 white rhinos reportedly died in Umfolozi during the very severe drought of 1933, when the total population numbered only about 300 animals (Player & Feely 1960; Walker *et al.* 1987).

The highest cementum line count obtained in tooth sections from white rhinos from the wild indicated an age of about 40 years (Hillman-Smith *et al.* 1986). The oldest zoo-kept animal, a female in the Pretoria zoo, was still alive aged 39 years in 1986, although appearing somewhat aged. Thus potential longevity may be estimated as about 45 years.

Summary

Megaherbivores generally show low adult mortality rates from natural causes, of the order of 2–5% per annum. Male mortality rates may be somewhat higher due to fighting injuries, and may be doubled by human hunting. Only giraffe are subject to significant predation as adults. Juveniles of all species are vulnerable to lions, tigers and perhaps hyenas for at least the first month or two. While all species may show episodically high mortality during severe droughts, the main effect is generally on calf survival. However, catastrophic mortality of adults has been recorded among elephants at Tsavo East in Kenya, and among hippos in the Kruger Park in South Africa. Potential longevity is 25 years for giraffe, but 35–60 years for other species.

Comparisons with smaller ungulates

Among many bovids the young lie out for the first month or two following birth, while among megaherbivores only giraffe show this pattern. In medium-sized ungulates nursing generally lasts about six months, compared with a year or longer among megaherbivores. Female bovids generally produce their first offspring between 1 and 3 years of age; and males become sexually potent at a similar age, although social maturity may be delayed until 4–8 years. Most female ungulates breed once annually, although in buffalo and zebra females fail to conceive some years; while among megaherbivores calving intervals span several years. Male bovids generally maintain prime breeding status for no longer than 2–3 years. Medium-sized ungulates show potential lifespans of 12–20 years, half as long as is typical of megaherbivores (Lent 1974; Mentis 1972; Murray 1982a; Owen-Smith 1984; Sinclair 1974).

Predation by carnivores is a significant source of mortality among adults of all ungulate species up to and including the size of African buffalo. Among megaherbivores only giraffe are vulnerable to predation mortality as adults, if human predation is excluded. Among elephants, rhinos and hippos, fighting among males and accidents such as becoming stuck in mud are the major source of mortality, apart from hunting. Population crashes have been documented for a number of medium-sized ungulate species during severe droughts (Schaller 1972; Sinclair 1977; Walker *et al.* 1987).

9

Body size and sociobiology

Introduction

This chapter considers the effects of large body size on social patterns, in particular (i) group size and structure; (ii) male dominance systems; (iii) female mate choice. Except for group size, these features are not readily characterized in numerical terms, and so cannot be related allometrically to body mass. Instead I will employ a cost/benefit analysis, assessing likely gains and losses in the factors determining evolutionary fitness, i.e. survival chances, reproductive contributions, and offspring survival. An inherent shortcoming of such an approach is that it does not adequately allow for possible interactions between these components (Crook & Goss-Custard 1972; Wilson 1975).

Grouping patterns

Jarman (1974) pointed out that among African bovids group size tends to increase with increasing body size. He explained this pattern in terms of the trade-off between the feeding costs of group formation, and the resultant anti-predation benefits. Because of their high specific metabolic rates, small antelopes are selective feeders on high quality plant parts. These are thinly scattered and quickly depleted. Large ungulates in contrast are relatively fiber-tolerant. They experience a much higher density of acceptable food, which is more uniformly distributed and depleted less by other animals foraging in the same area than is the food of small antelope. Intermediate sized species exhibit a gradient between these extremes. Hence the feeding cost of having close companions decreases with increasing body size.

This explains why large ungulates should be more tolerant of nearby conspecifics while foraging than smaller ungulates, but not why they should actively remain in a group. Jarman thus considered predation risks. Animals may benefit from having other animals nearby due to (i) more eyes to detect an approaching predator; (ii) the diluting effect of companions on the likelihood of being seized in an attack; (iii) the confusing effects of companions in disrupting the predator's attack; (iv) cooperative defense in warding off an attack. For small antelope (iv) is of no consequence, while (i) is of reduced benefit because most small ungulates occupy dense habitats. Furthermore, in thick vegetation animals tend to rely on concealment for predator evasion, and crypsis would be less effective if there were other animals nearby to attract the predator's attention. In contrast large ungulates, and in particular species occupying open grassland habitats, have nowhere to hide except amongst other animals. It is thus of greater benefit to be able to detect a stalking predator before it comes within attack range. The very largest species may furthermore be able to cooperatively ward off a predator by closing ranks and presenting powerfully backed horns outwards and vulnerable rears inwards.

Wittenberger (1980) emphasized the trade-off for females between the fitness gains from group formation in terms of individual survival, and the costs resulting from reduced offspring survival due to increased intraspecific competition for high quality food. For social ungulates he proposed that both adult survival and calf survival are raised by small increases in group size, but that beyond a certain group size the effects of food deprivation on offspring survival outweigh the predation benefits of group membership, at least for subordinate animals. He suggested that the particular form of these cost–benefit functions with increasing group size determined the optimal group size for a female of the species. Since male ungulates generally move independently of nursery groups, optimal group sizes should differ for males and females of the same species. Since males do not experience the effects of reduced feeding efficiency on offspring survival, Wittenberger's model implies that the optimal group size for a male should be somewhat larger than that for a female, unless other costs affect males.

Both Jarman's and Wittenberger's conceptual frameworks are based on the tradeoff between feeding costs and anti-predation benefits in relation to group size. Four possible patterns for these functions are sketched in Fig. 9.1. In all cases it is assumed that (i) predation risks decrease asymptotically as a function of group size, (ii) feeding effects on the survival of adults or offspring are linearly related to group size, and (iii) these factors interact multiplicatively, so that axes are appropriately scaled logarithmically. Fig. 9.1(a) is intended to depict the situation for a fairly small selectively feeding ungulate: the fitness component arising from anti-predation benefits rises quite rapidly with increasing group size, while the fitness component related to the effects of foraging efficiency on adult and offspring survival decreases

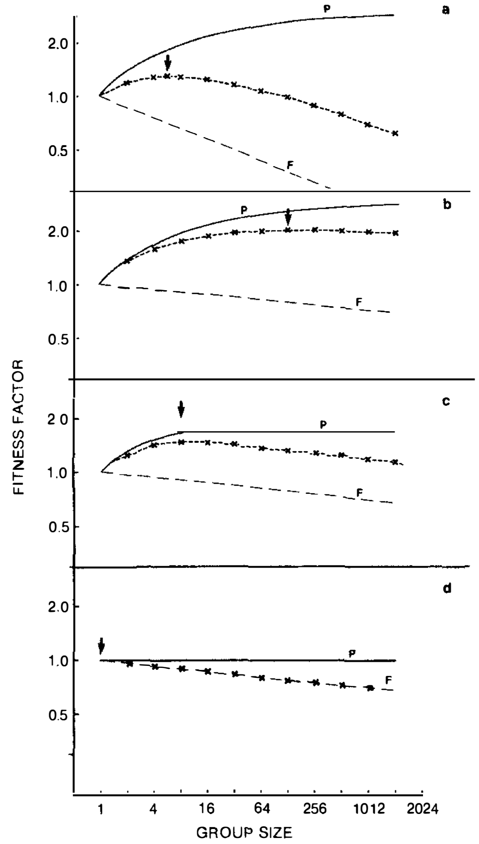


Fig. 9.1 Four hypothetical examples of the functional dependence of fitness components on group size. Solid lines (P) indicate the fitness factor resulting from predation risks; dashed line (F) indicates the fitness factor related to changing foraging efficiency. The product of these fitness components is indicated by the dotted-x curve. Arrows indicate the group size conferring maximum fitness. Example (a) is intended to represent a selectively feeding ungulate, (b) a less selective feeder, (c) a species with reduced anti-predation benefits, and (d) a species invulnerable to predation.

rather steeply with increasing group size. The optimal group size in this example lies in the range 4–8. Fig. 9.1(b) represents a larger ungulate, with similar anti-predation benefits, but with feeding costs less strongly influenced by group size. This leads to a rather larger optimal group size of about 100. In Fig. 9.1(c) feeding costs remain low, but anti-predation benefits are reduced, perhaps because they influence only adult survival, or solely offspring survival, rather than both. The outcome in this case is a small optimal group size of about 10. In Fig. 9.1(d) there are no anti-predation benefits associated with group formation, and the optimal group size is 1.

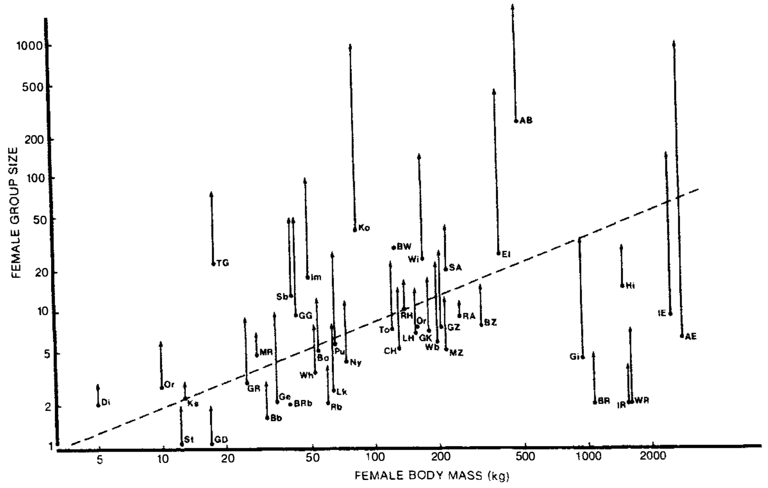


Fig. 9.2 Female group sizes for mainly African large herbivores in relation to body mass. Dot indicates the mean size of female–young groups, arrow the maximum group size recorded. Key to species labels given in Appendix I. Data from Anderson (1980), Attwell (1977, 1982), Backhaus (1959), Bigalke (1972), Conybeare (1980), Cumming (1975), David (1973, 1978), De Vos & Dowsett (1966), Douglas-Hamilton (1972), Dowsett (1966), Duckworth (1972), Dunbar (1979), Dunbar & Dunbar (1974), Duncan (1975), Eltringham (1977), Eltringham & Woodford (1973), Estes (1966, 1967), Estes & Estes (1974), Goddard (1967), Grobler (1973, 1974), Guy (1974), Hall-Martin (1975), Hendrichs (1971, 1975), Hendrichs & Hendrichs (1971), Hillman (1979), Irby (1977), Jacobsen (1973), Jarman & Jarman (1974), Jewell (1972), Joubert (1972, 1974, 1975), Joubert & Bronkhorst (1977), Jungius (1971b), Klingel (1967, 1974), Kok (1975), Kurt (1974), Laurie (1978), Laws *et al.* (1975), Leuthold (1970, 1971, 1974, 1976b, 1977b, 1979), Leuthold & Leuthold (1975), Murray (1980), Novellie (1975), Oliver *et al.* (1978), Olivier & Laurie (1974), Owen-Smith (1984), Penzhorn (1975), Rodgers (1977), Schenkel & Schenkel-Hulliger (1969a), Simpson (1974), Sinclair (1977), Spinage (1974), Van Lavieren & Esser (1980), Viljoen (1980), Von Richter (1972), Walther (1972b, 1978), Waser (1974), Watson (1969).

Regression (based on means):

(i) for species up to the size of African buffalo (AB), indicated by dashed line: $FEMGP = 0.43M^{0.64}$ ($R^2 = 0.38$, $N = 38$, $P < 0.001$).

(ii) all species: $FEMGP = 2.28M^{0.21}$ ($R^2 = 0.08$, $N = 45$, $P = 0.05$).

All bovids up to African buffalo size are vulnerable to predation even as adults. However, among megaherbivores (excepting giraffe) only immature animals are susceptible to non-human predation. Thus one might anticipate a dramatic drop in group size above a body mass of 1000 kg.

This prediction is indeed supported by the data on female group sizes for a wide range of large herbivores (Fig. 9.2). There is a significant positive correlation between mean female group size and body mass for species up to the size of African buffalo. But while African buffalo form large herds averaging about 250 animals, giraffe occur in small groups numbering typically about 4–5 animals, while rhino females of all species are generally accompanied only by a single offspring. However, hippos and elephants appear anomalous in forming somewhat larger groups.

The hippo situation is a special one in that feeding costs are not a factor during the daytime when groups are formed. Daytime aggregations are simply related to the restricted availability of suitable pools relative to the densities of animals supported by adjacent grasslands. At night hippos forage solitarily.

The formation of small but cohesive family units by elephants of both species could be due to (i) a greater susceptibility of elephant calves to predation, relative to other megaherbivores, (ii) an increased benefit from cooperative defense in warding off a predator attack, or (iii) some other factor influencing group formation not taken into account in the model outlined above.

Elephant calves are indeed likely to benefit from being protected in the middle of family units while the adult females form a protective ring. However, it is not obvious why rhino calves would not gain a similar advantage. White rhino groups including subadults do adopt a defensive rump-to-rump formation, which is clearly advantageous in the event of attacks by lions or hyenas. However, a white rhino cow drives away an older offspring as if the presence of the latter would be more of a detriment than a benefit to the protection of a small calf.

The sizes of all-male groups provide a test as to whether some factor besides offspring protection from predation might be involved in group formation. The mean size of all-male groups tends to rise with increasing body size, but the trend is much weaker than that shown by female–young groups, and is marginally non-significant statistically (Fig. 9.3). The so-called bachelor groups formed by Thomson's gazelle and African buffalo are similar in size, despite a 25-fold difference in body mass; while males of species as large as roan antelope are quite commonly solitary. Since males invariably form much smaller groups than females with young, it is evident that the anti-predation benefits of group formation for offspring survival are a more important factor than feeding costs, contrary to Wittenberger's (1980) emphasis.

Among megaherbivores, adult males are generally solitary in giraffe, rhinos, and hippos on land. African elephant bulls frequently occur in small all-male groups, while Asian elephant males also sometimes join up together. Unlike family units, these bull groups are open in membership.