COMPUTER MODELLING THE SERENGETI-MARA ECOSYSTEM

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Submitted in accordance with the requirements for the degree of
Doctor of Philosophy

The University of Leeds
School of Biology

October 2003

The candidate confirms that the work submitted is her own and that appropriate credit has been given where reference has been made to the work of others.

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"Everything you see exists together, in a delicate balance…you need to understand that balance and respect all the creatures…from the crawling ant to the leaping antelope.

When we die, our bodies become the grass. And the antelope eat the grass. And so we are all connected in the great circle of life."

~

Taken from Disney's
The Lion King

THESIS
CONTAINS
CD/DVD

ACKNOWLEDGEMENTS

Huge thanks directed at Bryan Shorrocks, who has supervised and supported me endlessly and at many times beyond the call of duty. His enthusiasm for this subject is contagious and I hope he never stops dreaming of Africa.

Thanks to Mpala Research Centre in Laikipia Kenya and their many researchers, for showing me that lions really do exist and so much more. I now have a wonderful collection of my own personal death-defying stories that I am sure I will be telling even when I am really really old.

Special thanks to, Dr. Melanie Hatcher, Zoe Davies, and Dan (The Oracle) Hoare, who were always able to explain things. Thanks to Bill Gates and Microsoft Excel. I am most grateful for its ability to cope with my model. Cheers to all my friends and colleagues in Leeds from University & my various employments. Congratulations for putting up with me for so long. Particular mention goes to Steve D'Souza, who will always be considered my saviour and biggest bestest bud.

Chocolate covered thanks to my parents, who have supported me to the best of their abilities. I am truly grateful to my dad for all his good advice, having faith in me and reading all my chapters over and over again. Not forgetting my little squizzer and Claire Dunthorne, whose love and friendship were imperative to my sanity whilst living with the folks.

A substantially large amount of thanks, with an infinitely large amount of love thrown in, goes to Ted Bodsworth. Every page of this thesis is a direct result of his support, help and love, and for that I am forever indebted.

ABSTRACT

At present, the viability of biodiversity in most of the remaining natural areas of the world is primarily threatened by human encroachment. This has led to an increased demand for active conservation. However, in order to devise and implement appropriate management strategies for a particular area, a specific understanding of ecosystem function is required. Creating a simulation model using available research data may provide a way to achieve this.

In this thesis, the construction of a comprehensive model delineating the dynamics of the Serengeti-Mara ecosystem is initiated. Using the abundance of research data collected on this ecosystem over the last 40 years, the processes involved in setting-up such a model are investigated. First, a basic foundation, accommodating the spatial and temporal variation in climate and physiography across the Serengeti region, is established. The relationship between grass growth and rainfall is then incorporated, along with the mechanisms concerned with limiting grass availability, the subsequent survival and recruitment of grazing herbivores and finally, the influence of predation upon those herbivores.

The model, even in these early stages of development, adequately depicted dynamics equivalent to those in the Serengeti-Mara ecosystem, indicating that the methods used were appropriate. It was found that grass availability was not the primary factor influencing the overall dynamics of grazing herbivores within the ecosystem, and only migratory wildebeest appeared to be strongly influenced by this factor throughout the time-scale of the model. It was suggested that other factors were responsible for regulating the majority of herbivore populations. By identifying where further research is required to increase our understanding of this particular ecosystem's function, the model demonstrates its effectiveness as an analytical tool. For the long-term conservation of the Serengeti-Mara ecosystem and other similar ecosystems, this reveals that the construction of such models is certainly beneficial, if not essential.

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ABBREVIATIONS

In this thesis, due to the high level of repetition of certain terms, a number of abbreviations are commonly used. These are always explained when the term is first introduced into the text, but below is a summary of those most frequency used.

BMR	Basal Metabolic Rate
CP	Crude Protein
FpA	Food per Animal
I	Intake
I_M	Minimum Intake
ITCZ	Intertropical Convergence Zone
MMR	Minimum Metabolic Rate
Mya	Million years ago
PVA	Population Viability Analysis
RMR	Relative Metabolic Rate

CHAPTER 1: THE SERENGETI-MARA ECOSYSTEM

1.1 INTRODUCTION

According to Hopkins (1965) a savannah is a type of vegetation consisting predominately of grasses. Glover (1968), Menaut (1983) and Gichohi *et al.* (1996) go on to state that in addition to the characteristic understorey, an overstorey of trees and/or shrubs may also be present. This type of biome is particularly extensive in Africa and has long been recognised for sustaining extraordinarily high faunal diversity (Figure 1.1; Cumming 1982; Owen-Smith 1982; Sinclair 1983; Estes 1991; Gichohi *et al.* 1996; du Toit & Cumming 1999). For instance, it boasts no less than 96 vertebrate species heavier than 2 kg (Dorst & Dandelot 1970), including an abundance of large predators and 76 species of bovid typical of savannah habitats (Estes 1991; Kingdon 1997).

This remarkable diversity is the consequence of an evolutionary history unique to Africa, and as such, has attracted both scientific and economic attention (Gichohi *et al.* 1996; du Toit & Cumming 1999; Table 1.1). In particular, Tanzania and Kenya in East Africa, possess some of the largest remaining areas of savannah to still contain a rich diversity and abundance of wildlife (Rodgers & Swai 1988; Baldus *et al.* 1997; Prins & Olff 1998; Figure 1.2). Both countries have remained thinly populated, especially Tanzania which contains some 20 million people living on 364,886 square miles of land (Alexander 1986). This has meant that even with ever-expanding human settlement and agricultural development, Tanzania still contains extensive tracts of relatively undisturbed wildlife habitat. Furthermore, the country's commitment to conserving its wildlife heritage is considered to be outstanding despite being an economically poor developing nation (Wasser 1987). The Tanzanian government has maintained a relatively effective conservation policy compared to many of the other African countries, and established an impressive system of conservation areas (Baldus *et al.* 1997; Wasser 1987). It has, at present, 11 national parks (including the Ngorongoro Conservation Area) and 17 game reserves, all of which prohibit settlement and cultivation, as well as several game controlled areas and forest reserves, where both wildlife and habitats receive protection (IUCN 1974; Lamprey 1975). These represent well over 20% of the country's total area and this figure is still increasing (Wasser 1987; Rodgers & Swai 1988; Figure 1.3).

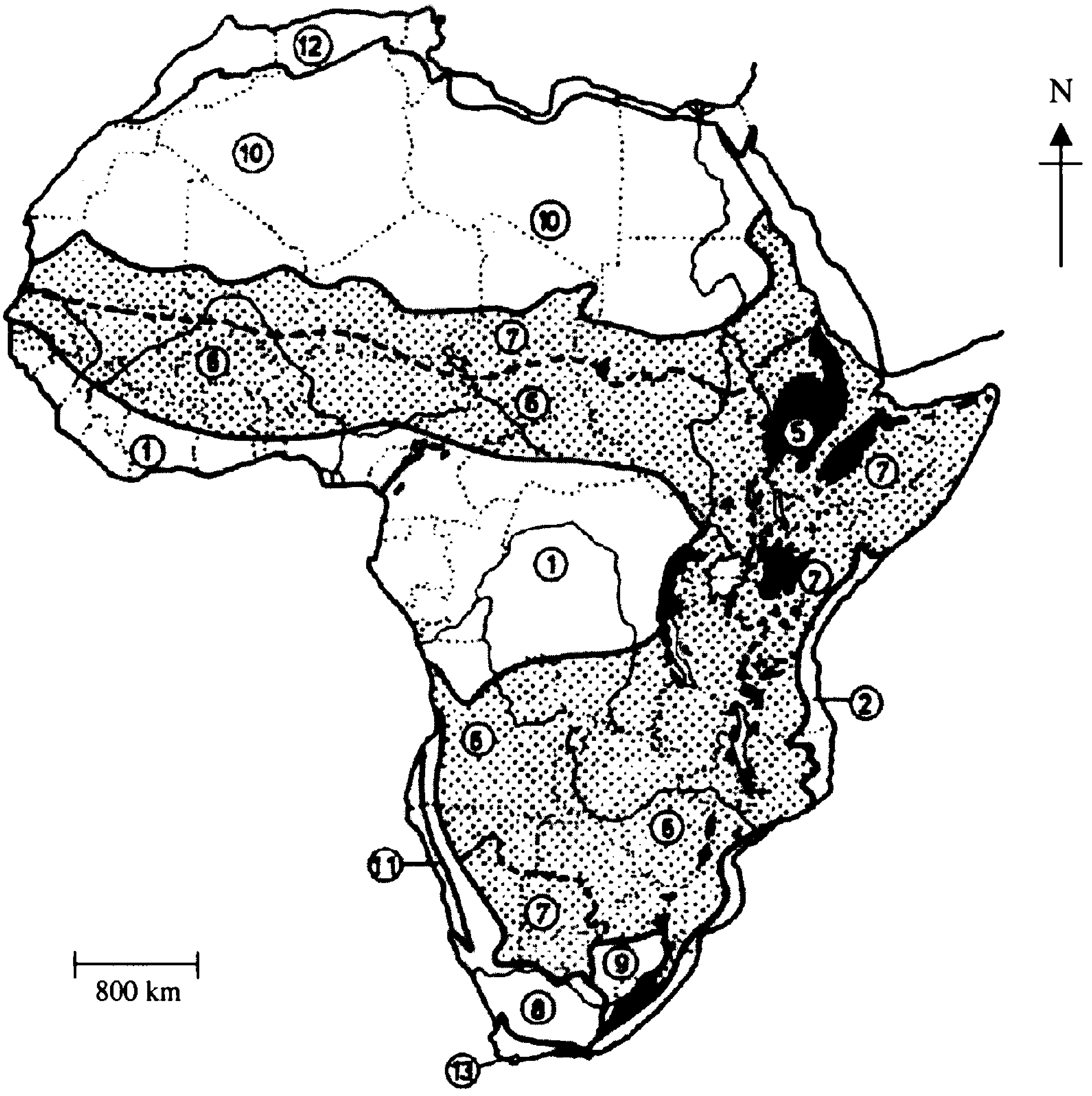

Figure 1.1 Vegetation map of Africa (14° W to 50° E, 40° N to 40° S) indicating those regions (stippled) broadly referred to as savannahs. Numbered vegetation types include: (1) lowland rainforest, (2) East Africa lowland rainforest, drier forest and evergreen bush, (5) afro-montane vegetation, (6) broad-leaved woodland and wooded grassland, (7) thorn (*Acacia*) woodland, wooded grassland and semi-desert vegetation, (8) Karoo/Namib semi-desert shrubland, (9) grassland, (10) Sahara Desert, (11) Namib Desert, (12) Mediterranean vegetation and (13) Cape sclerophyllous shrubland, bushland and thicket (Cumming 1982).

Table 1.1 Ungulate biomass and species richness in some national parks and other protected areas (Sinclair & Norton-Griffiths 1979; Huston 1994; Kingdon 1997).

Location		**Habitat**	**Number of Ungulate Species**	**Live biomass (tonnes/ km^2)**
Africa	Tarangire Game Reserve, Tanzania	Open *Acacia* savannah	14	1.1
	Kafue National Park, Zambia	Tree savannah	19	1.3
	East Tsavo National Park, Kenya	Open *Commiphora Acacia* woodland	13	4.4
	Nairobi National Park, Kenya	Open savannah	17	5.7
	Serengeti National Park, Tanzania	Open and tree savannah	27	8.2
	Rwenzori National Park, Uganda	Open savannah and thickets	11	12.0
	Rwenzori National Park, Uganda	See above, overgrazed	11	27.8 - 31.5
	Virunga National Park, Zaire	Open savannah and thickets, overgrazed	11	23.6 - 24.8
South Asia	Gir Forest, Gujarat, India	Dry deciduous woodland and tree savannah	6	0.4
	Wilopattu National Park, Sri Lanka	Open forest and scrub	7	0.7
	Kanha National Park, Madhya Pradesh, India	Open *Shorea robusta* forest and grass meadows	10	0.9 - 1.2
	Karnali-Bardia National Park, Terai, Nepal	Open *Shorea robusta* forest and grass flood plain	6	2.8 - 3.1
	Kaziranga Wildlife Sanctuary, Assam, India	Grass flood plain	9	3.8
	Chitawan National Park, Tarai, Nepal	Tall grass and riverine forest	6	18.5
South America	Estacion Biologica de los Llanos, Masaguaral, Venezuela	Mosaic of savannah types	2	0.3

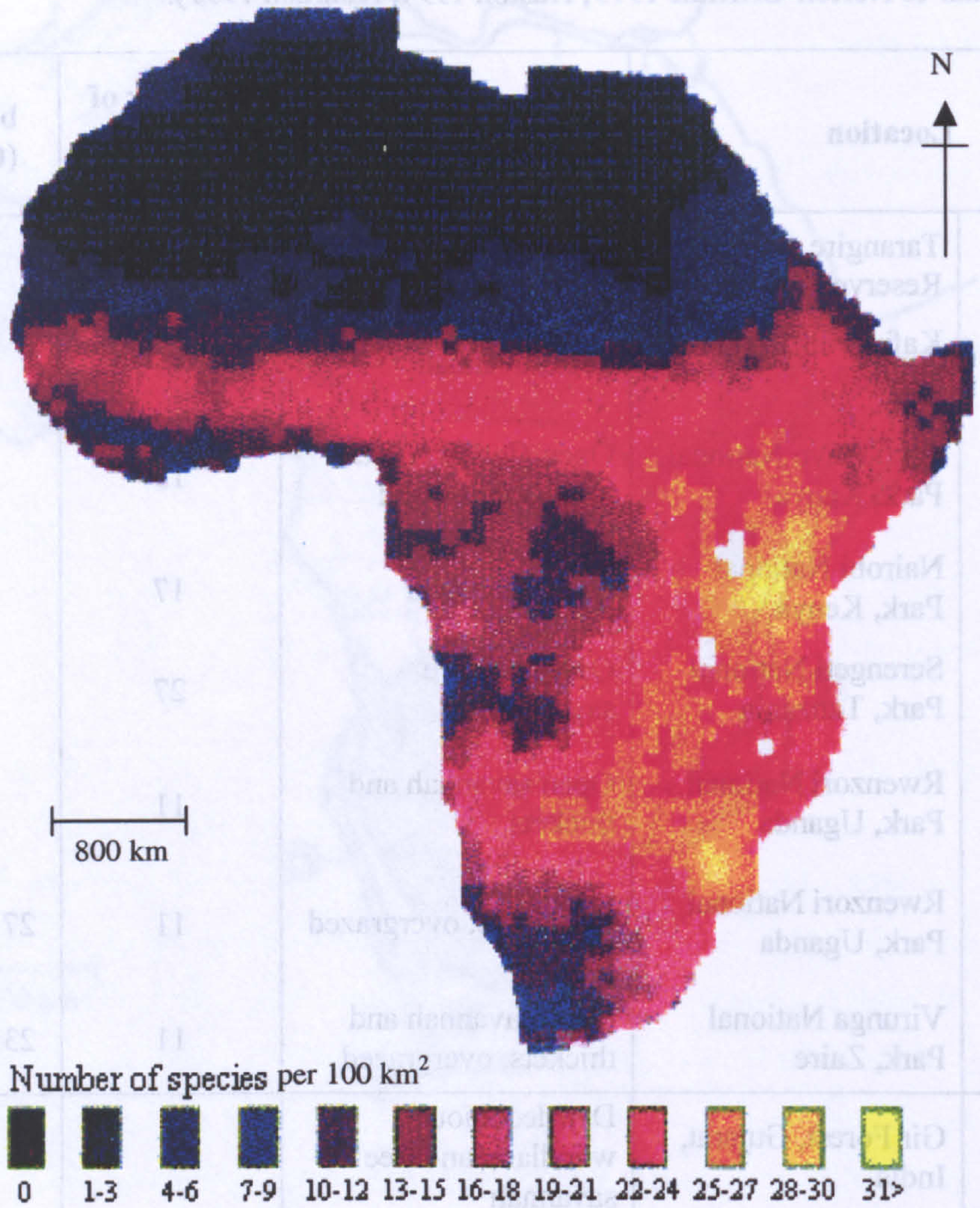

Figure 1.2 Spatial variation in the regional species richness of grazers larger than 2 kg in continental Africa (14° W to 50° E, 40° N to 40° S; Prins & Olff 1998). Note the biodiversity hotspots in East African savannahs.

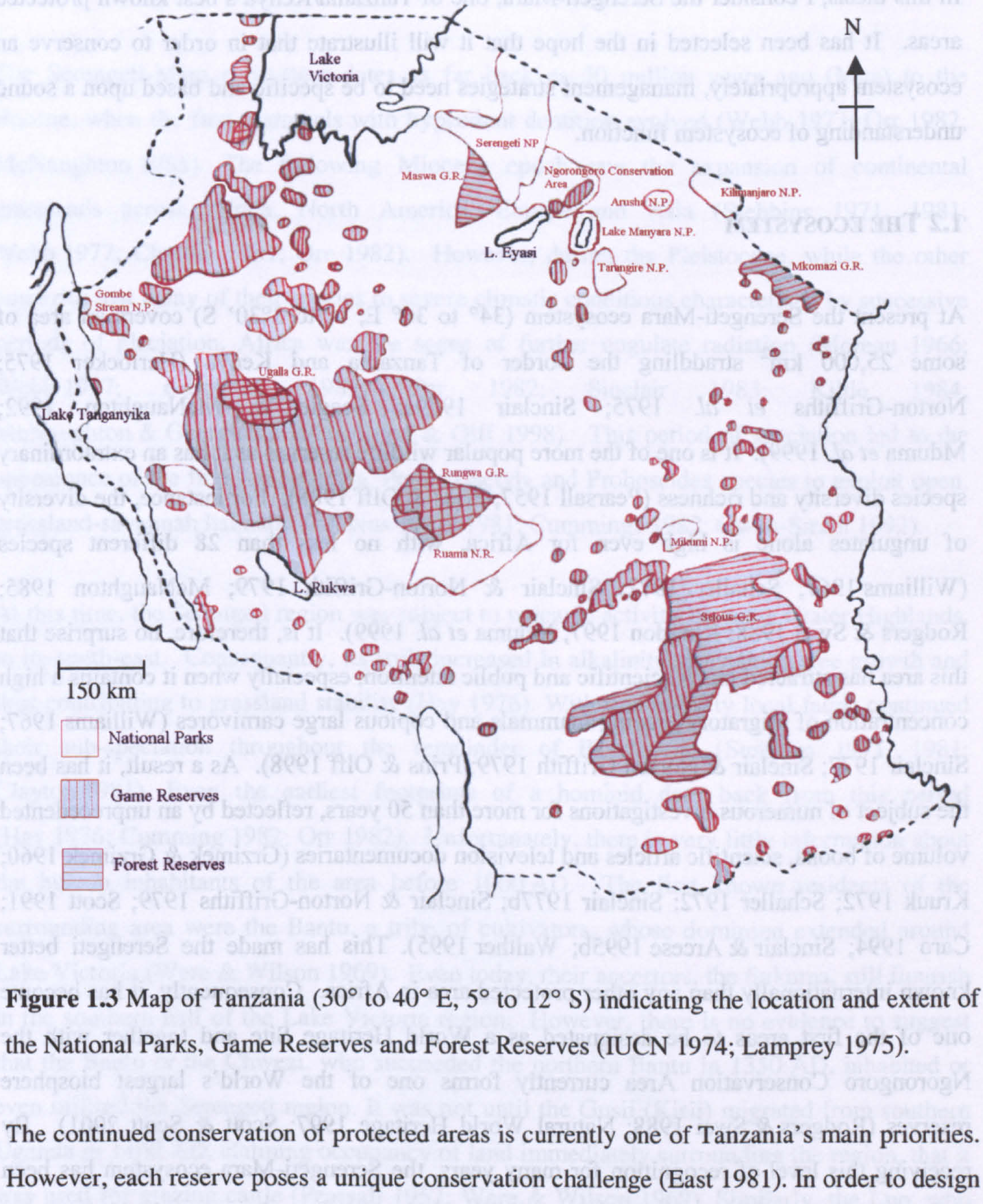

Figure 1.3 Map of Tanzania (30° to 40° E, 5° to 12° S) indicating the location and extent of the National Parks, Game Reserves and Forest Reserves (IUCN 1974; Lamprey 1975).

The continued conservation of protected areas is currently one of Tanzania's main priorities. However, each reserve poses a unique conservation challenge (East 1981). In order to design appropriate management strategies, the history, species dynamics, structure and function of each area needs to be considered. For instance, Arusha National Park in north-eastern Tanzania is one of the smallest parks (134 km^2; Williams 1967; IUCN 1974; WCMC 1985). Despite its size, its vegetation varies considerably, from lacustrine to montane types, due to an extreme change in altitude within the area (from 1,500 m to over 4,500 m). In contrast, Selous Game Reserve in southern Tanzania covers a considerably larger area (44,800 km^2), but it is fairly uniform in its habitat composition, mainly consisting of deciduous woodlands and wooded grasslands (Williams 1967; IUCN 1974; Pateman 1987; WCMC 1998).

In this thesis, I consider the Serengeti-Mara, one of Tanzania/Kenya's best known protected areas. It has been selected in the hope that it will illustrate that in order to conserve an ecosystem appropriately, management strategies need to be specific and based upon a sound understanding of ecosystem function.

1.2 THE ECOSYSTEM

At present the Serengeti-Mara ecosystem (34° to 36° E, 1° to 3°30' S) covers an area of some 25,000 km^2 straddling the border of Tanzania and Kenya (Herlocker 1975; Norton-Griffiths *et al.* 1975; Sinclair 1979a; Seagle & McNaughton 1992; Mduma *et al.* 1999). It is one of the more popular wildlife reserves as it has an extraordinary species diversity and richness (Pearsall 1957; Prins & Olff 1988). For instance, the diversity of ungulates alone is high even for Africa, with no less than 28 different species (Williams 1967; Schaller 1972; Sinclair & Norton-Griffith 1979; McNaughton 1985; Rodgers & Swai 1988; Kingdon 1997; Mduma *et al.* 1999). It is, therefore, no surprise that this area has attracted much scientific and public attention, especially when it contains a high concentration of migratory grazing mammals and copious large carnivores (Williams 1967; Sinclair 1977; Sinclair & Norton-Griffith 1979; Prins & Olff 1998). As a result, it has been the subject of numerous investigations for more than 50 years, reflected by an unprecedented volume of books, scientific articles and television documentaries (Grzimek & Grzimek 1960; Kruuk 1972; Schaller 1972; Sinclair 1977b; Sinclair & Norton-Griffiths 1979; Scott 1991; Caro 1994; Sinclair & Arcese 1995b; Walther 1995). This has made the Serengeti better known internationally than any other protected area in Africa. Consequently, it has become one of the first areas to be designated as a World Heritage Site and together with the Ngorongoro Conservation Area currently forms one of the World's largest biosphere reserves (Rodgers & Swai 1988; Natural World Heritage 1997; Scott & Scott 2001). By receiving this level of recognition for many years, the Serengeti-Mara ecosystem has been fortunate. In contrast, many other natural habitats have now been fragmented and destroyed (Pearsall 1957; Sinclair & Norton-Griffith 1979; McNaughton 1985; Western & Gichohi 1993; Gichohi *et al.* 1996).

1.2.1 History

The Serengeti-Mara ecosystem dates as far back as 50 million years ago (Mya) to the Eocene, when the first mammals with hypsodont dentition evolved (Webb 1977; Orr 1982; McNaughton 1985). The following Miocene epoch saw the expansion of continental grasslands across Africa, North America, Europe and Asia (Stebbins 1971, 1981; Webb 1977; Clayton 1981; Orr 1982). However, during the Pleistocene, while the other countries lost many of their species to severe climatic conditions characterised by successive periods of glaciation, Africa was the scene of further ungulate radiation (Moreau 1966; Webb 1977; Cumming 1982; Orr 1982; Sinclair 1983; Kiltie 1984; McNaughton & Georgiadis 1986; Prins & Olff 1998). This period of speciation led to the appearance of the first Artiodactyla, Perissodactyla and Proboscidea species to exploit open, grassland-savannah habitats (Stebbins 1971, 1981; Cummings 1982; Owen-Smith 1992).

At this time, the Serengeti region was subject to volcanic activity from the Crater Highlands, to its south-east. Consequently, its soils increased in alkalinity, preventing tree growth and thus contributing to grassland stability (Hay 1976). With this stability local fauna continued their sub-speciation throughout the remainder of Pleistocene (Stebbins 1971, 1981; Clayton 1981). Even the earliest footprints of a hominid date back from this period (Hay 1976; Cumming 1982; Orr 1982). Unfortunately, there is very little information about the human inhabitants of the area before 1000 AD. The first known residents of the surrounding area were the Bantu, a tribe of cultivators, whose dominion extended around Lake Victoria (Were & Wilson 1969). Even today, their ancestors, the Sukuma, still flourish in the southern half of the Lake Victoria region. However, there is no evidence to suggest that the Bantu or the Chwezi, who succeeded the northern Bantu in 1350 AD, inhabited or even utilised the Serengeti region. It was not until the Gusii (Kisii) migrated from southern Uganda in 1400 AD, claiming occupancy of land immediately surrounding the region, that it was used for grazing cattle (Pearsall 1957; Were & Wilson 1969). Similarly, the Luo, who appeared from the Sudan Republic in the late 16th century, having succeeded the Chwezi, also grazed their cattle here (Were & Wilson 1969). This status quo continued until the Maasai migrated along the Rift Valley from northern Kenya in the mid 18th century (Grizimek & Grzimek 1960). Their extreme practice of grazing huge herds of cattle across the whole area, whether it was under their effective control or not, caused conflict in the region, and the Gusii were soon forced from the area (Pearsall 1957; Talbot & Talbot 1963; Were & Wilson 1969; Sankan 1973).

By the late 19th century, conflict between the Maasai and neighbouring tribes had reached an apex (Were & Wilson 1969). Fuelled by drought, famine, smallpox and cattle disease the Maasai population was left weak and severely diminished. As a result, much of the land under their occupation became desolate, although three small sub-populations remained in the Serengeti area, one in the so-called Maasai-Mara, another in the Loliondo region and the third in Ngorongoro Conservation Area (Pearsall 1957; Were & Wilson 1969; Hayes *et al.* 2001a). All three continued their grazing regime within the Serengeti.

However, it was not long before the area was recognised for its recreational value by Europe. The first European to actually see the Serengeti plains was the German explorer Baumann in 1892 (Turner 1962; Were & Wilson 1969). By 1909, spurred on by encouraging reports, hunters where beginning to notice the area's potential. Within ten years, hunting safaris had become so popular that many species were on the brink of local extinction (Turner 1962; Lamprey *et al.* 1967; Were & Wilson 1969; Hayes *et al.* 2001b). Fortunately, this situation was recognised by the Tanganyikan Government under the British administration, who established a 2,286 km^2 game reserve in what is now the southern and eastern region of the Serengeti (Turner 1962; Lamprey *et al.* 1967; Were & Wilson 1969). In 1930, another region to the west towards Lake Victoria, became a 'closed reserve', in which the hunting of particular species was prohibited (currently known as a 'partial game reserve'; Turner 1962). This area's boundaries were further extended in 1932, and by 1937 additional species of game were put under protection, including all carnivores, giraffe, buffalo and roan antelope. Three years on, this area was combined with the game reserve and given protected area status under the Game Ordinance (Turner 1962; Natural World Heritage 1997). Shortly after this, the 2,590 km^2 'Northern Extension' was added.

Meanwhile, the lease on the area to the south east of the Serengeti, including the Ngorongoro Crater, expired in 1928, reverting it to the crown (Turner 1962). This land was declared a complete reserve, and subsequently all hunting was prohibited. Its borders were extended in 1936, again in 1937 and soon after the area was made into a conservation unit, referred to as the Eastern Serengeti (Turner 1962). By 1951, the Serengeti National Park was established, made up of the southern and eastern Serengeti (Natural World Heritage 1997). In 1958, attempts were made to prohibit any land-use of the western Serengeti, much to the disapprobation of the inhabiting Maasai (Turner 1962). Following this, the Serengeti's boundaries were realigned in 1959 to include the area known as the Lamai Wedge between Banagi and the Kenya border (Alexander 1986). Conversely, the Ngorongoro Crater and its surrounding area was excised from the Serengeti National Park to become a independent conservation area (Alexander 1986). In 1965, the Mara Reserve in Kenya was formed and deemed part of the Serengeti-Mara ecosystem, which by 1967 had reached its present standing, with the addition of a small area north of the Grumeti River to the Serengeti National Park.

Since its establishment, UNESCO proposed the Serengeti National Park to be a World Heritage Site. This was formally announced in 1981 with its acknowledgement as a Biosphere Reserve, along with Ngorongoro Conservation Area, under UNESCO's Man and the Biosphere Programme (Sinclair 1995a; Natural World Heritage 1997). The Serengeti is currently the largest national park in Tanzania, representing 14,763 km^2 of the Serengeti-Mara ecosystem's core area ostensibly protected from poaching and human encroachment (Williams 1967; Braun 1973; Herlocker 1975; Seagle & McNaughton 1992; Natural World Heritage 1997). The ecosystem itself extends into a number of different game reserves and conservation areas, including the Ngorongoro Conservation Area, Maswa game reserve, Grumeti/Ikoma, Ikorongo, and Loliondo game controlled areas in Tanzania, as well as the Masai Mara National Reserve and adjoining group ranches in Kenya (Herlocker 1975; Norton-Griffiths *et al.* 1975; Sinclair 1995a; Baldus *et al.* 1997; Natural World Heritage 1997; Mduma *et al.* 1999; Figure 1.4).

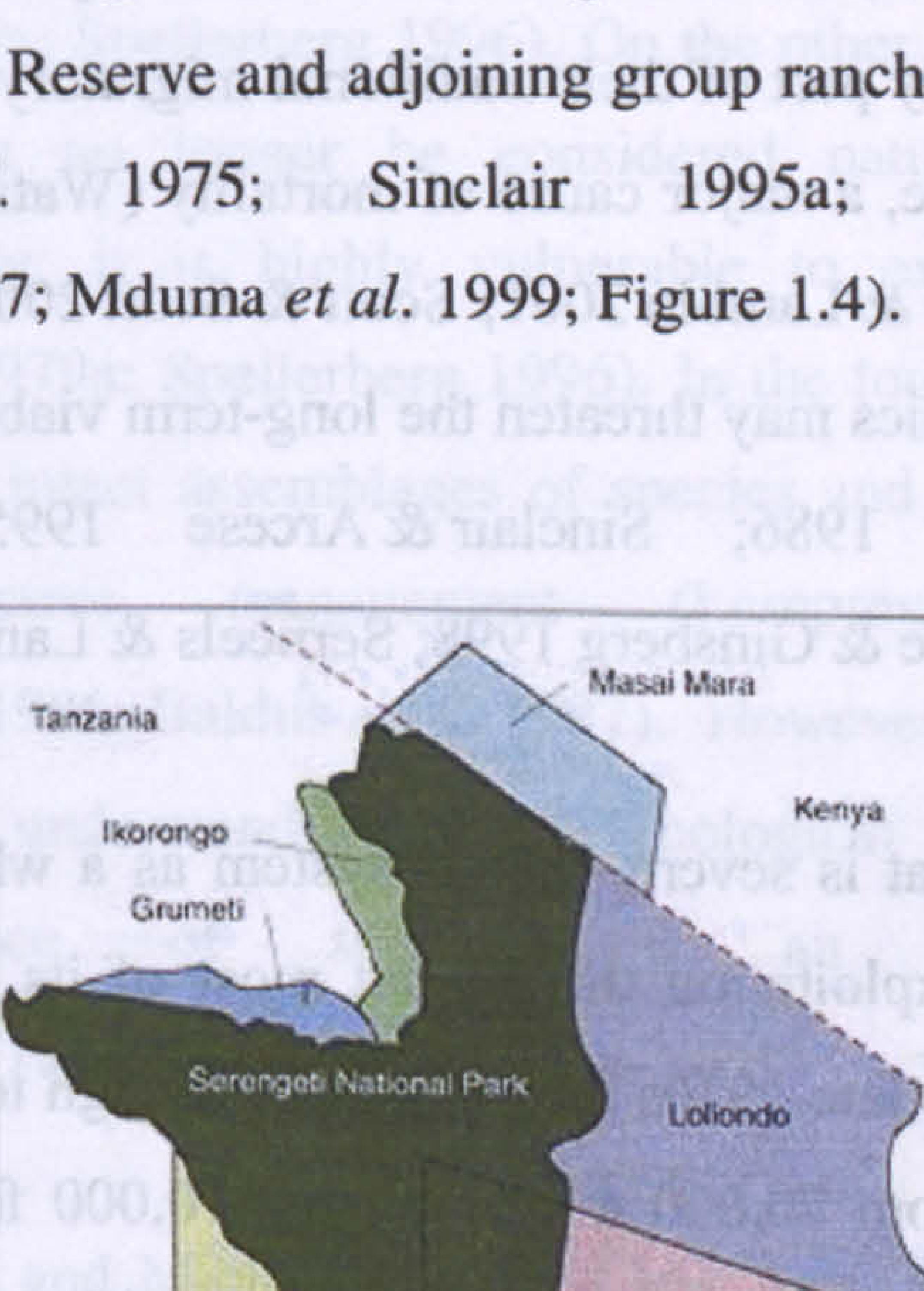

Figure 1.4 Map of the Serengeti–Mara ecosystem, identifying the Serengeti National Park and surrounding protected areas (Wolanski *et al.* 1999)

1.3 PRESENT CONSERVATION

Although the Serengeti-Mara ecosystem receives a certain degree of protection from its designated status, a passive approach is no longer adequate since its surrounding area contains an increasing, burgeoning human population, a growing demand for agricultural land and heavy poaching (Watson 1965; Hofer *et al.* 1993; Western & Gichohi 1993; Pressey 1996; Natural World Heritage 1997; Caro *et al.* 1998; Homewood *et al.* 2001; Ottichilo *et al.* 2001). For example, since the ecosystem's borders were determined, large-scale wheat fields have replaced much of the forest and grassland along the northern border of the reserve and overpopulation around Lake Victoria is continually forcing settlers towards the western border (Alexander 1986; Hofer *et al.* 1993; Scott & Scott 2001). Initially, the surrounding unreserved land would have acted as a natural buffer zone on which the ecosystem's fauna partially relied upon as habitat (Franklin 1993; Mbano *et al.* 1995). At present, the continued use of land adjacent to the western border by migratory herbivores, the only part of their traditional migratory route unprotected, conflicts with humans and is, therefore, a major cause of mortality (Watson 1966; Kurji 1975, 1976; Mbano *et al.* 1995; Serneels & Lambin 2001; Scott & Scott 2001). The subsequent impact this has on population dynamics may threaten the long-term viability of the whole ecosystem (McNaughton & Georgiadis 1986; Sinclair & Arcese 1995b; Kat *et al.* 1996; Baldus *et al.* 1997; Woodroffe & Ginsberg 1998; Serneels & Lambin 2001).

Although this particular threat is severe, the ecosystem as a whole has been vulnerable to human encroachment and exploitation throughout most of its history (Hofer *et al.* 1993; Caro *et al.* 1998). During the late 1970s the number of foreign tourists visiting the Serengeti National Park plummeted from 70,000 a year to just 10,000 following the closure of the Tanzania/Kenya border (Baldus *et al.* 1997). This concomitant loss of revenue precipitated in a 60 % decline in anti-poaching patrols to the extent that by 1986 only one vehicle covered the entire Serengeti (Scott & Scott 2001). The combined effects of the increased human population to the west of the park and the lack of anti-poaching patrols resulted in an invasion of the Serengeti by poachers. Consequently, by 1978, 50 % of the area's estimated 700 black rhinoceros (*Diceros bicornis*) had perished (Alexander 1986; Scott & Scott 2001). Within the space of a year they were reduced to a small population in the Ngorongoro Crater (Baldus *et al.* 1997). Buffalo (*Syncerus caffer*) and African elephant (*Loxodonta africana*) were also severely poached with heavily armed motorised gangs reducing the Serengeti's 2,500 elephants to a mere 1,000 (Baldus *et al.* 1997; Scott & Scott 2001).

Since the mid-1980s, there has been a degree of economic recovery and relative stability following the reopening of most of the Kenyan border in 1983 (Alexander 1986; Baldus *et al.* 1997). In June 1989, the Tanzanian government launched Operation Uhai. This intense, short-term, nation-wide crackdown on poaching was successful at the time in preventing the Serengeti-Mara ecosystem being irreversibly altered through species loss. This incident reinforces the notion that the existence of a legally established protected area does not ensure the survival of the fauna or habitats it contains (Lamprey 1975; Norton-Griffiths *et al.* 1975; Hanks 1979; East 1983; Belsky 1985; Seagle & McNaughton 1992; Meffe & Carroll 1994; Gros *et al.* 1996; Scott & Scott 2001). This has led to an ongoing debate regarding the most appropriate methods of conservation (Spellerberg 1996). With limited resources, conservationists must prioritize the allocation of funds and this has caused controversy. One view is that protection is of foremost importance and therefore anti-poaching and education are a primary concern. Once human-induced pressures are removed, it can be assumed that an ecosystem will maintain its natural state independently (Sinclair 1979a; Spellerberg 1996). On the other hand, it has been argued that an isolated ecosystem can no longer be considered natural and will not function independently. Consequently, it is highly vulnerable to external factors and random stochastic events (Sinclair 1979a; Spellerberg 1996). In the long-term, it may, therefore, be more beneficial to preserve intact assemblages of species and their habitats as functioning ecosystems through active management (Lamprey 1975; Allen 1981; McNaughton & Georgiadis 1986; Baldus *et al.* 1997). However, in order to design effective management strategies, an understanding of the ecological principles that promote the diversity and abundance of species in an ecosystem is required (McNaughton & Georgiadis 1986; Gros *et al.* 1996).

Since 1957, when Bernhard and Michael Grzimek began the first studies of the Serengeti-Mara ecosystem, data has been accumulating regarding the ecosystem and its function. Following the formation of the Serengeti Wildlife Research Institute (SWRI) in 1966, continued studies in a range of topics involving biology and physiography have amassed ecological data on virtually every facet of the Serengeti-Mara ecosystem over the last 40 years (Lamprey *et al.* 1971; Schaller 1972; Herlocker 1975; Frame *et al.* 1979; Chesson & Warner 1981; Bell 1982; McNaughton 1983; East 1984; McNaughton & Georgiadis 1986; Scott 1991; Murray *et al.* 1992; Burrows *et al.* 1994; Burrows 1995; Ginsberg *et al.* 1995).

1.4 PHYSIOGRAPHY

During the Eocene epoch an uplifting along the rift valley created the high interior plateau on which the Serengeti area lies (Cooke 1968; Kendall 1969). These tectonic events also governed the formation of Lake Victoria along the western edge of the Serengeti, and the formation of the Loita Hills, Gol Mountains, Lake Eyasi escarpment and Crater Highlands along the eastern and southern borders. These features act as natural barriers, partially isolating the ecosystem (McNaughton 1983; Mduma *et al.* 1999). However, it is Lake Victoria, into which the majority of the region's rivers drain, and the volcanic activity in the Crater Highlands, that have led to the majority of physiographic variation within the Serengeti. Three regions can be crudely distinguished (Belsky 1985; Gereta & Wolanski 1998; Figure 1.5).

I. *The Serengeti Plains* stretch westward from the Crater Highlands and Gol Mountains within the Ngorongoro Conservation Area, into the south-east of the Serengeti National Park. The region's highest altitude is 1,850 m on the far-east side, and the area slopes from here to a low point of 920 m in the west (Williams 1967; Sinclair 1977b). The Mbalageti River is one of two rivers that originates on the plains and drains 2,680 km^2 within the Serengeti (Schaller 1972; Gereta & Wolanski 1998; Wolanski *et al.* 1999). In contrast, the Olduvai River drains eastwards through the Olduvai Gorge to the base of the Ngorongoro Highlands (Talbot & Talbot 1963; McNaughton 1983).

II. *The northern extension* stretches from Seronera (2 °26'S, 34 °48'W) towards the Loita plains into the Maasai Mara National Reserve (Broten & Said 1995). Altitudes range from 1,500 m at Seronera to 1,800 m near the Loita plains (Talbot & Talbot 1963; Williams 1967; Croze 1974 a, b; McNaughton 1985; Broten & Said 1995). Overall, the area consists of gently sloping ridges and valleys from which many small tributaries drain into the region's three main rivers. In the upper half, the Mara River forms the main drainage system for an area of 10,300 km^2 (Kendall 1969; Broten & Said 1995; Gereta & Wolanski 1998; Wolanski *et al.* 1999). The Grumeti River, originating from the Loliondo area to the east, covers a more central catchment area of 11,600 km^2, while the Orangi River provides the southern watershed (Schaller 1972; Gereta & Wolanski 1998).

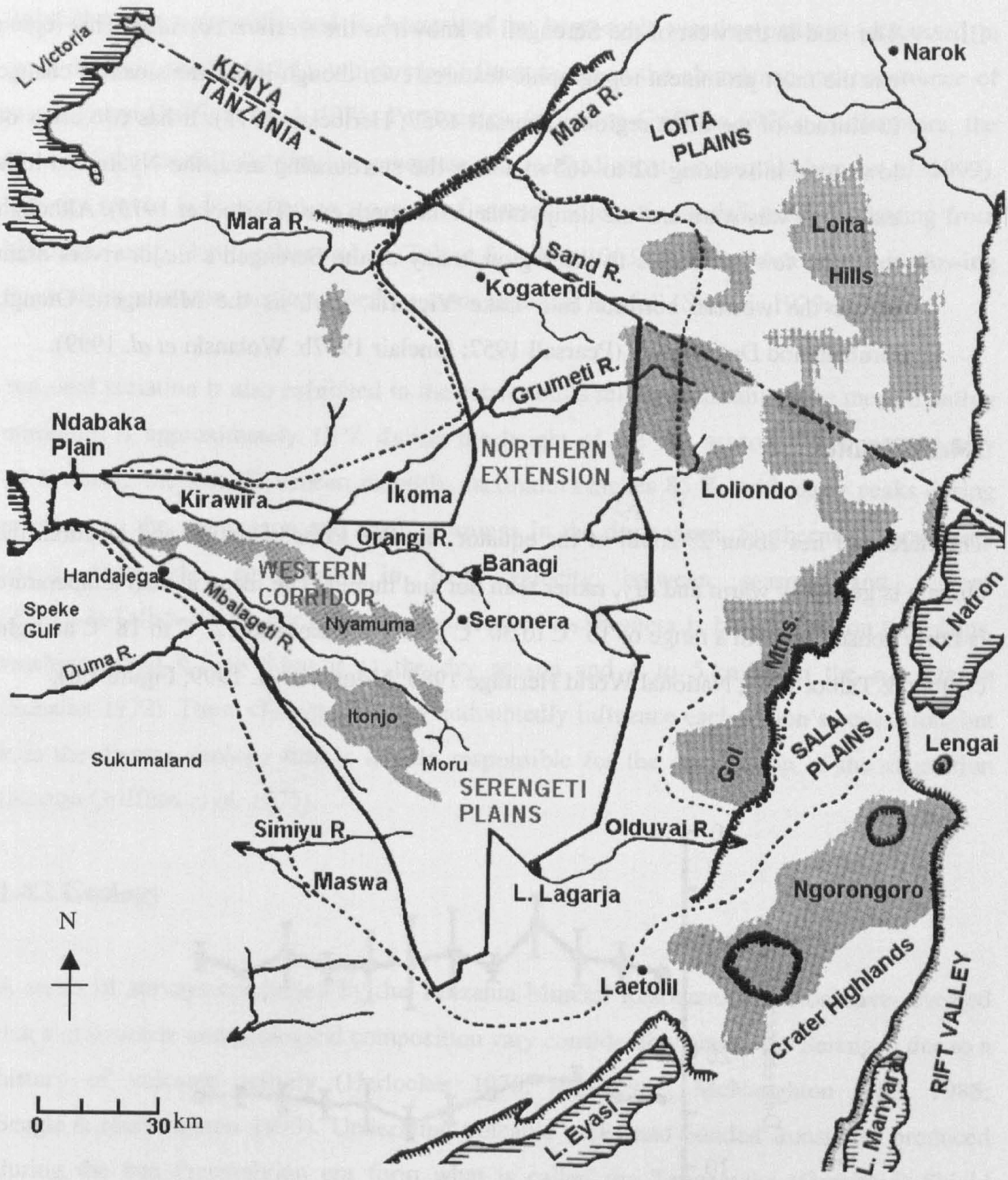

Figure 1.5 Map of the Serengeti-Mara ecosystem (dotted outline), with hills shaded and the Serengeti National Park bounded by a solid line. The location of major rivers and lakes are also illustrated.

III. The land in the west of the Serengeti is known as the *western corridor*. This region has the most prominent topographic features even though it has the smallest change in altitude of the three regions (Pearsall 1957; Herlocker 1975). It has two areas of low stony hills rising 62 to 465 m above the surrounding area, the Nyamuma hills extending westward and the Itonjo hills in the south-east (Herlocker 1975). Although there are few tributaries in the region, many of the Serengeti's major rivers drain across the western corridor into Lake Victoria, such as the Mbalageti, Orangi, Grumeti and Duma rivers (Pearsall 1957; Sinclair 1977b, Wolanski *et al.* 1999).

1.4.1 Climate

The Serengeti lies about 2° south of the equator, but due to its elevation and location, the climate is generally warm and dry, rather than hot and humid. The mean annual temperature is fairly constant within a range of 15 °C to 30 °C during the day and 12 °C to 18 °C at night (Talbot & Talbot 1963; National World Heritage 1985; Mduma *et al.* 1999; Figure 1.6).

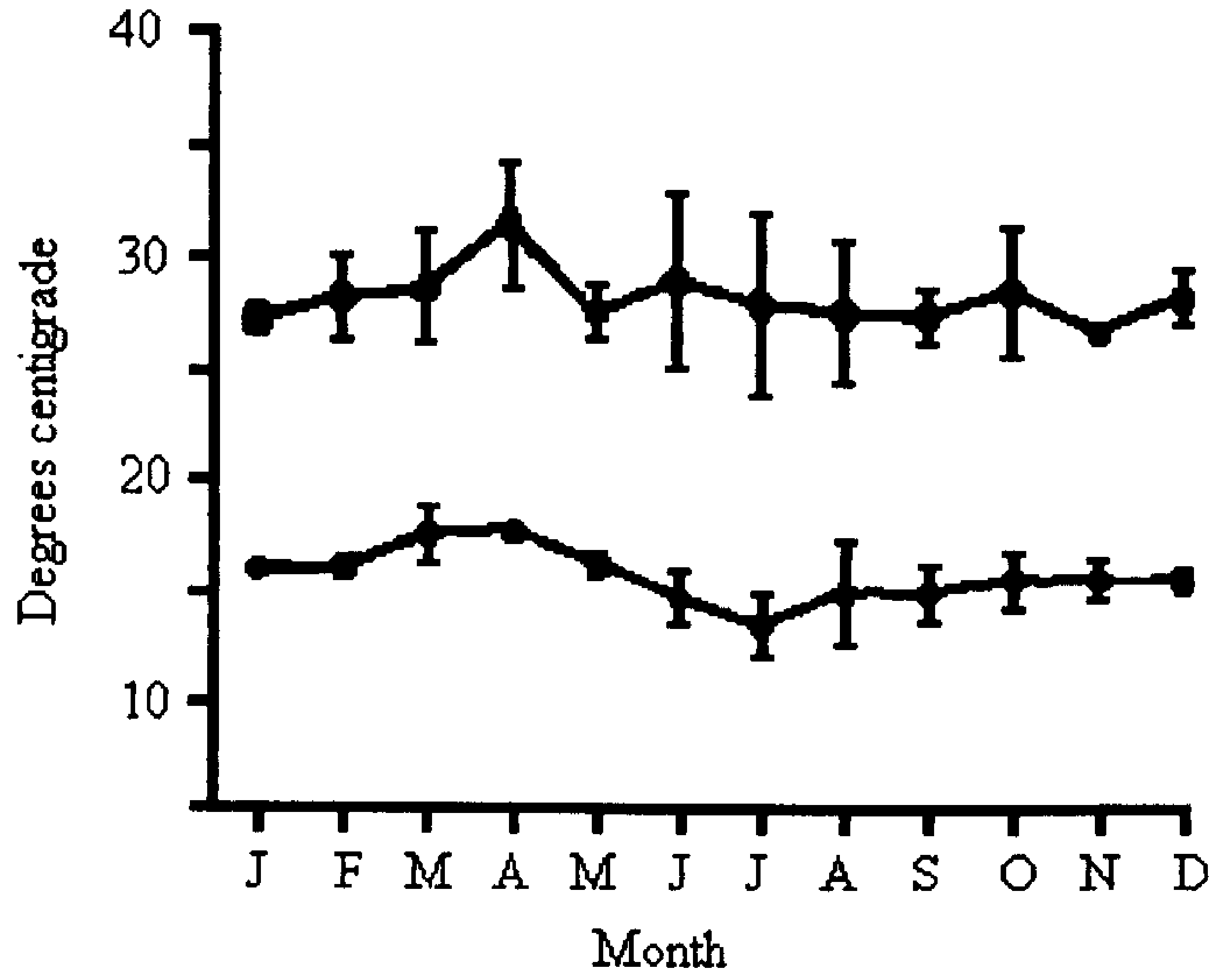

Figure 1.6 Mean monthly (and SD) maximum (upper line) and minimum (lower line) temperatures for the Serengeti-Mara ecosystem from March 1980 to December 1983 (Caro 1994).

Rainfall varies temporally and is determined by large-scale weather patterns (discussed in more detail in section 3.2.1), which create fluctuations in the abundance and occurrence of rain (Norton-Griffiths *et al.* 1975; Pennycuick & Norton-Griffiths 1976). Furthermore, the nature of the rainfall distribution generates two fairly distinct seasons (Mduma *et al.* 1999). The dry season is identified as a period of sparse and erratic rainfall generally lasting from May/June until October/November (Talbot & Talbot 1963; McNaughton 1985). Following this is the wet season, distinguished by more abundant rainfall (Sinclair 1979a).

Seasonal variation is also exhibited in the ecosystem's relative humidity. The mean monthly minimum is approximately 15 % during the height of the dry season, and approximately 40 % during the wet. The mean monthly maximum reaches 85 %, with daily peaks during evenings in the wet season and early mornings in the dry season. Furthermore, prevailing winds from the east vary in their velocity between seasons and regions (Talbot & Talbot 1963). For example, wind speed at Seronera is half of that on the plains, reaching about 6.5 to 8 km/hr in the dry season and 4 to 5 km/hr in the wet season (Schaller 1972). These climatic features undoubtedly influence each region's vegetation, but it is the diverse geology that is largely responsible for the distribution of the vegetation (Norton-Griffiths *et al.* 1975).

1.4.2 Geology

A series of surveys conducted by the Tanzania Mineral Resources Division have revealed that soil structure and geological composition vary considerably across the Serengeti due to a history of volcanic activity (Herlocker 1975; Bell 1982; McNaughton 1983, 1985; Seagle & McNaughton 1993). Underlying volcanic rocks and banded ironstones produced during the late Precambrian era form what is called the Tanganyika (Granitoid) Shield (Pearsall 1957). An orogenic event in the Eocene epoch then distorted this shield, giving rise to features such as the Gol Mountains and Loita Hills (Cooke 1968). On the Serengeti plains evidence of this distortion appears in the form of kopjes (inselbergs). These are rocky outcrops produced in the areas where pressure has forced the shield upwards (Pearsall 1957; Williams 1967; Croze 1974 a, b; Herlocker 1975).

During the Pleistocene age, volcanic activity continued in the Crater Highlands (Hay 1976). From these eruptions, aerially discharged material blown westward settled across the Serengeti plains. Consequently, volcanic ash covered the Tanganyika shield, forming the characteristic soils found in the region (Pearsall 1957). Continued activity from the Lengai volcano has maintained this soil composition by replenishing it regularly (eruptions have been recorded in 1917, 1921, 1940 and 1966; Pearsall 1957; Talbot & Talbot 1963; Anderson & Talbot 1965; McNaughton 1983). As a result, the soils are high in salinity and alkalinity with a loose granular composition (Bell 1982). They are, therefore, highly porous and their salts are leached out easily. This has led to the formation of the petrocalcic horizon, a calcium carbonate hardpan created when salts are re-deposited about 1 m below the soil's surface (Watson & Kerfoot 1964). Due to the composition of the top layers, erosion is common, particularly in the dry season when the plains become virtual deserts (Sinclair 1979a). This aridity is enhanced further as the region's water sources either dry-up or become highly saline (Gereta & Wolanski 1998; Wolanksi *et al.* 1999).

Across the plains, soil structure changes from coarse-grained sandy soils on the Salai plains in the east to fine-grained clay soils to the north-west (Pearsall 1957; Seagle & McNaughton 1993). This progression is due to prevailing winds carrying the lighter, more mobile volcanic material further (Sinclair 1979a). As a result, soils towards the north-west are able to retain water for longer and contain less soluble material, such as sodium and calcium (Pearsall 1957). This is reflected in the hardpan, as its continuity and hardness depends on the extent of leaching. For example, on the northern plains, soils are deeper (about 2 m) and although calcium carbonate concretions do occur, the petrocalcic horizon is absent.

In contrast to this, the soils in the northern extension are formed from an underlying quartzofelspathic parent rock. Consequently, they are relatively infertile, sandy soils, low in salinity and alkalinity, and deep in the absence of a hardpan (Milne 1935; Herlocker 1975; Bell 1982; Seagle & McNaughton 1993). The region also contains more fertile black-clay alluvial soils, produced from silt build-up in flood basins and valley bottoms (Talbot & Talbot 1963; Ruess & Halter 1990).

In the western corridor, soils to the east are characteristically red, derived from granite, sandstone and quartzite gneisses, a feature that is particularly prominent on the Nyamuma and Itonjo hills (Talbot & Talbot 1963; Herlocker 1975). Further west, heavy black cotton clays of sedimentary origin overlay granite rock-beds (Pearsall 1957). Where both soils are present, the contrast between the red soils on the slopes of the hills and the dark sedimentary soils in the valley bottoms is striking (Talbot & Talbot 1963).

1.4.3. Vegetation

As the three regions vary in their topography and soil composition, it is not surprising that this has influenced the physiognomy of the vegetation (life form, density, cover, height, etc) in each (Norton-Griffiths *et al.* 1975; Walker & Noy-Meir 1982; McNaughton 1983; Gichohi *et al.* 1996). For instance, the plains are predominantly open grassland with few trees, most of which are located on or around kopjes (Sinclair 1975; Belsky 1985). In contrast, the western corridor and northern extension have a mosaic of vegetation types ranging from dense woodland to open grassland (Pearsall 1957; Herlocker 1975; McNaughton 1985; Figure 1.7).

The plains are primarily grassland, lacking trees due to the presence of the petrocalcic horizon. It is impermeable, allowing only plants with shallow root systems, such as grasses, to thrive in the soil above it (Walker & Noy-Meir 1982). Tree growth is impeded further by the high alkalinity of this soil, which also quickly dries out in the absence of rain (Anderson & Talbot 1965; Norton-Griffiths *et al.* 1975; Walker & Noy-Meir 1982; McNaughton 1985). Grass composition follows a similar pattern due to the progression in soil structure across the plains. Towards the east, where the petrocalcic horizon is well formed, dwarf growth forms of couch grass (*Digitaria macroblephora*), *Cynodon dactylon* and pan dropseed grass (*Sporobolus icoclados*, an indicator of saline soils) thrive, while grass-like sedges, such as *Kyllinga nervosa* are also common (Pearsall 1957; Watson & Kerfoot 1964; Braun 1973; Sinclair 1975; Schmidt 1975; McNaughton 1983; Belsky 1985; National World Heritage 1997; McNaughton & Banyikwa 1999). Here, basal cover tends to be relatively low (averaging 10 % annually), as low rainfall levels during the dry season precludes virtually all plant growth/survival (Kreulen 1975; Sinclair 1979a; Natural World Heritage 1997). As the soil becomes deeper across the plains, roots are able to penetrate the interstices between the less continuous hardpan (Watson & Kerfoot 1964). Consequently, taller grass forms flourish, as well as other species, such as *Andropogon greenwayi,* which thrives in the lower salinity and alkalinity (Watson & Kerfoot 1964; Braun 1973; Schmidt 1975; Belsky 1985; McNaughton 1983, 1985; Seagle & McNaughton 1993). The deeper soils also support extensive areas of herbs, primarily *Indigofera basiflora* and *Solanum incanum* (McNaughton 1983). Overall, average basal cover is approximately 30 %, reflecting this area's milder environment (Kreulen 1975). This increases further north, where tall grass species thrive, such as red oats (*Themeda triandra*) and *Pennisetum mezianum,* while herb abundance is relatively low (Pearsall 1957; Watson & Kerrfoot 1964; Braun 1973; Kreulen 1975; Schmidt 1975;

Sinclair 1975; McNaughton 1983, 1985; Belsky 1985; Seagle & McNaughton 1993; McNaughton & Banyikwa 1999).

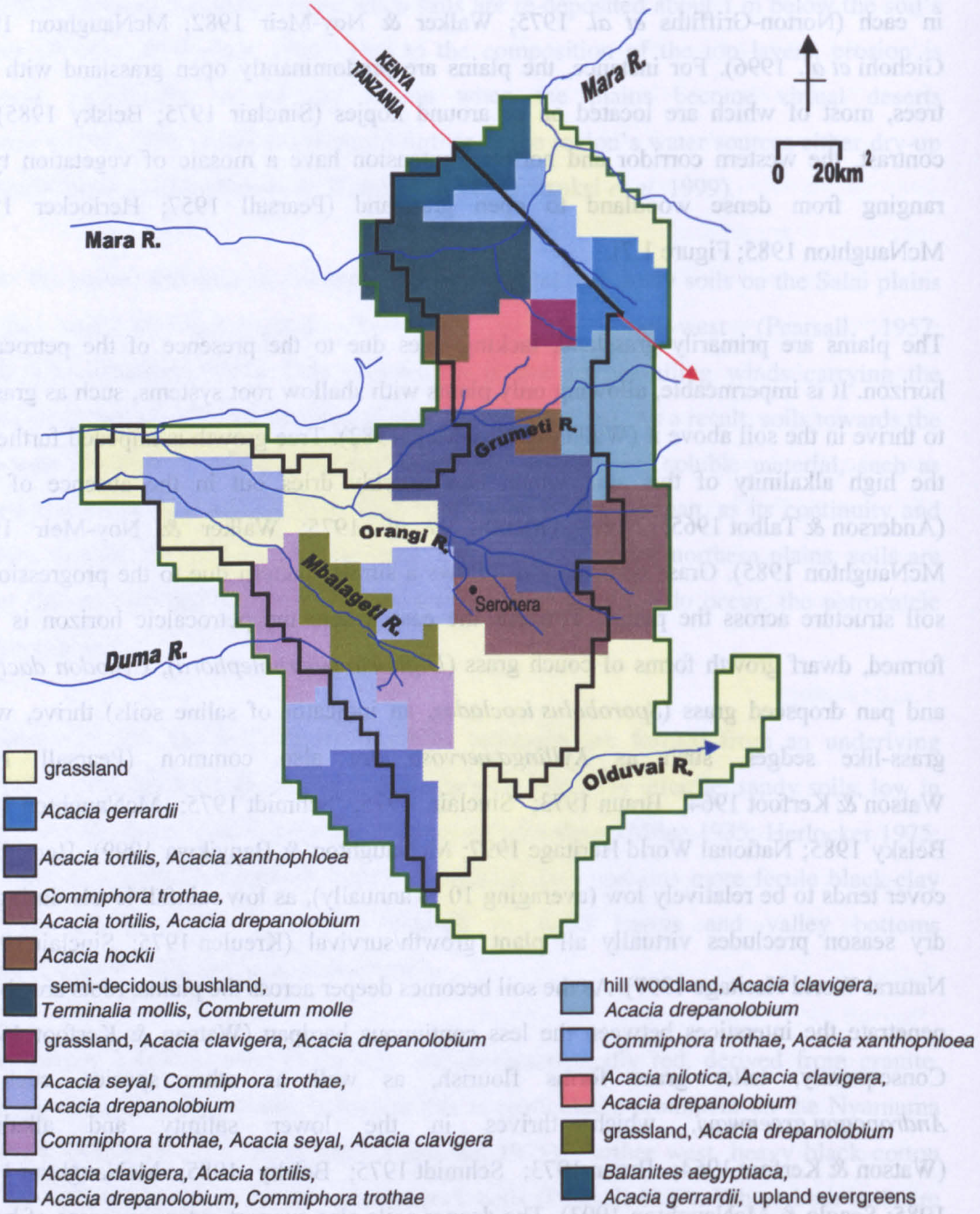

Figure 1.7 Vegetation types within the Serengeti-Mara ecosystem. After Herlocker (1975).

In contrast to the plains, the northern extension and western corridor are, for the most part, wooded, signifying the lack of a petrocalcic horizon. Both regions are comprised of many different vegetation types, some of which are unique to each region and some shared (Herlocker 1975). The most common vegetation is *Acacia* woodland, constituting 7,260 km^2 overall (Croze 1974a, b; Herlocker 1975). However, there are 38 *Acacia* species present in the Serengeti, each with specific habitat and topographical requirements (Pearsall 1957; Talbot & Talbot 1963; Croze 1974 a, b; Herlocker 1975; Natural World Heritage 1997). In the northern extension, the whistling thorn (*A. drepanolobium*) and the umbrella tree (*A. tortilis)* frequently dominate valley bottoms and lower slopes (Talbot & Talbot 1963; Herlocker 1975; Ruess & Halter 1990). In contrast, species such as *A. clavigera,* prefer well-drained soils on upper slopes and ridges, particularly in the Itonjo Hills (Herlocker 1975).

The understorey and grass stratum within the majority of these *Acacia* woodlands is fairly similar. The former commonly consists of widely scattered bushes of *Grewia fallax* and *Cordia ovalis*. Where it is dense, the grass stratum is dominated by less sun-tolerant species, including panic grass (*Panicum* sp.*)*, thatching (*Hyperthelia* sp.), citronella (*Cymbopogon* sp.) and dropseed (*Sporobolus* sp.; Talbot & Talbot 1963; McNaughton & Banyikwa 1999). In a more open understorey, tall grass species, such as *Themeda triandra* and *Eustachys paspaloides* dominate well drained soils, while *Digitaria macroblephara* and *Chloris pycnothrix* prefer poorly drained soils along open valley bottoms (Pearsall 1957; Vesey-Fitzgerald 1970). Overall, basal cover for these grasses varies from 20 to 60 %, but generally averages 45 % (Anderson & Talbot 1965).

Both regions contain areas of other distinct vegetation types. For instance, the northern extension has patches of relict evergreen forest, consisting of broad-leaved evergreen and sclerophyllous woody species, such as *Diospyros asyssinica, Lecaniodiscus fraxinifolius* and *Elaeodendron buchananii* (Herlocker 1975). Here, *Croton dichogamus* and *Teclea trichocarpa* constitute the bush stratum, while the herbaceous understorey is characterised by the broad-leaved grass, *Setaria chevalieri*. The patchy distribution of this type of forest is due to its high demand for water and susceptibility to fire. It, therefore, occurs in valley bottoms along seepage lines and riverbanks, such as the Mara River, or on ridge tops and slopes with particularly deep soils (Herlocker 1975). There are also patches of the open deciduous woodlands once prominent in the region. These broad-leaved trees, such as *Combretum molle* and *Terminalia mollis*, are now confined to ridge tops and upper slopes (Herlocker 1975). The understory is quite open, although dominated by deciduous thorn trees (*Acacia nilotica* and *A. hockii*), while its lower stratum includes long grasses, such as *Hyparrhenia filipendula*, *Ditheteropogon* sp. and *Loudetia* sp. (Herlocker 1975).

In the western corridor, riparian strips of forest and bush thicket occur along the major watercourses. These are commonly surrounded by grassland on the region's poorly drained clay floodplains (Norton-Griffiths *et al.* 1975; Ruess & Halter 1990). Here, very tall grasses (2 m high), such as *Panicum maximum* are prevalent in areas that remain flooded for long periods. Otherwise coarser grasses, such as *Pennisetum mezianum*, predominate (Pearsall 1957).

This varied and diverse composition of vegetation within the Serengeti is not entirely influenced by the area's spatial and temporal characteristics. It is the interspecific interactions between both flora and fauna that has shaped their coevolution and subsequent diversity and composition (McNaughton & Georgiadis 1986; Ritchie & Olff 1999).

1.5. FAUNA

According to geological records, the coevolution of mammals and plants began during the Eocene with the appearance of the first herbivorous mammals (Cooke 1968; Estes 1991; MacDonald 2001). They were able to digest plant cell walls using microbial symbionts (bacteria and protozoa) maintained and contained in a fermentation chamber in the gut (Owen-Smith 1992; Hofmann 1989). A group of herbivores, collectively known as Artiodactyla, evolved as foregut fermenters with chambers developed from the oesophagus or anterior portion of the stomach (Clemens & Malioy 1982; Langer 1976; van Hoven 1978; Hofmann 1989). This group developed the ability to accelerate the digestion of cellulose by regurgitating and re-chewing partially digested material from a specially adapted fermentation chamber called the rumen (Fosse 1982; Kingdon 1982a; Owen-Smith 1992; Twine 2002). In contrast, hindgut fermenters, the Perissodactyla and Proboscidea, used the caecum, a blind sac branching from the junction of the small and large intestines (Langer 1984; Owen-Smith 1992; Hofmann 1989). They compensated for their lower efficiency by increasing food intake and gut passage rates, thus maximising extraction of nutrients per unit time rather then per unit food consumed (Crawley 1983; Estes 1991; Illius & Gordon 1992; Twine 2002).

The selection pressures of herbivory led to the evolution of plant defensive and protective adaptations (Owen-Smith 1982). Of the two major groups of angiosperms, the dicotyledons generally evolved anti-herbivore defences, while the principal evolutionary response of monocotyledons was meristem relocation (Jarman 1974; Owen-Smith 1982). In particular, those of the Gramineae family, evolved the ability to compensate for the damaging effects of herbivory by increasing vegetative production from their protected inter-calary meristems

(Jameson 1963; Jarman 1974; Ryle & Powell 1975; McNaughton 1979b). Mammalian herbivores diversified in response, evolving features to aid in the procurement and digestion of specific types of plant material (Owen-Smith 1982). For instance, 'browsers' share a similar dentition and feed primarily on dicotyledonous plants (Hofmann 1989). They tend to have lower-crowned molars with prominent cusps for dissecting the leaves and stems of dicotyledons. In contrast, 'grazers' generally exhibit finely ridged surfaces on high-crowned molars for grinding the fine and fibrous leaves typical of graminoids (Estes 1991). There are also a number of common characteristics in the structure of the digestive tract between 'grazers' and 'browsers' (Owen-Smith 1982; McNaughton & Georgiadis 1986; Hofmann 1989; Iason & van Wieren 1999). 'Grazers' evolved a capacious fermentation chamber, narrow ostia and moderate surface papillation to cope with the slowly fermenting graminoid leaves (Owen-Smith 1982; McNaughton & Georgiadis 1986; Hofmann 1989). In comparison, 'browsers' developed relatively smaller chambers with profuse papillae and larger connecting openings to process the faster digesting dicotyledons (Hofmann 1973, 1989; Owen-Smith 1982, 1992; McNaughton & Georgiadis 1986). Comparable differences are likely to exist among hindgut fermenters, but this remains undocumented.

The coevolution between herbivores and plants continued into the Oligocene, by which time, herbivore speciation had led to the appearance of many ancestral Proboscidea, Perissodactyla and Artiodactyla species (Moreau 1966, Cooke 1968; Stebbins 1971, 1981; Web 1977; Cumming 1982; Orr 1982; MacDonald 2001). During the Eocene, the later order consisted of relatively small (< 5 kg) forest frugivores and omnivores (Estes 1991). However, as the climate cooled during the Oligocene, fruit and non-fibrous vegetation production became seasonal. Artiodactyla reciprocated by diversifying both in size and specialisation (Cooke 1968). They first reached Africa in the early Miocene, just as favourable climatic conditions prompted the expansion of grasslands over much of the country (Cooke 1968; Stebbins 1971, 1981; McNaughton 1979; Cummings 1982; Estes 1991). As these grasslands spread and diversified into many topographically different areas, their superior ability to digest green grass allowed the ruminants to do the same. They soon became the dominant herbivores, and by the late Miocene, had branched into two families, the Giraffidae and the Bovidae (the hollow-horned ruminants). The latter underwent the most successful of the ungulate radiations, diversifying into 11 distinct tribes, with a total of 26 bovid genera existing by the early Pleistocene (Moreau 1966; Webb 1977; Cumming 1982; Orr 1982). Estes (1991) attributes this success to the bovids' ability to specialise more narrowly and efficiently than any other family of herbivores. By tailoring size, feeding apparatus, digestive systems and dispersal patterns for a particular set of ecological conditions they have effectively partitioned African ecosystems into narrow niches (Hofmann 1989).

1.5.1 Family Bovidae

Currently, the Serengeti-Mara ecosystem accommodates 9 of the Bovidae tribes, with a total of 18 different species (Brashares *et al.* 2000; MacDonald 2001). Species of the Cephalophini tribe, commonly called duikers, have specialised in forest fruit- and foliage-eating (Kingdon 1997). Their ancestry is relatively unknown as no fossil records predate the Pleistocene, by which time they were already well established (Kingdon 1982a; Estes 1991; Brashares *et al.* 2000; MacDonald 2001). The available fossil records do show that duikers radiated to fill every available size, class and type of habitat, monopolising the ruminant-frugivore niche (Kingdon 1982a, 1997; Sinclair 1983; Estes 1991; Stuart & Stuart 1997). This niche is currently occupied in the Serengeti by the blue duiker (*Cephalophus monticola*) and common (grey or bush) duiker (*Sylvicapra grimmia*; Kingdon 1982a, 1997; East 1988; Hofmann 1989; Estes 1991; Stuart & Stuart 1997; Plate 1a-b).

The dwarf antelopes of the Neotragini tribe are considered to have invaded forests after the duiker radiation, filling the vacant understorey folivore niche (Sinclair 1983; Hofmann 1989; Estes 1991; Brashares *et al.* 2000). In the Serengeti, Kirk's dik dik (*Madoqua kirkii*) generally inhabits areas with close cover, while the steenbok (steinbuck) (*Raphicerus campestris*) and oribi (*Ourebia ourebi*) favour grasslands dotted with bushland and light woodlands (Kingdon 1982a, 1997; East 1988; Estes 1991; Plate 1c-e). Oribi are also adapted grazers, reducing the competition with their browse-preferring tribe member, the steenbok (Hofmann 1989; Kingdon 1982a, 1997; du Toit 1993; Mduma & Sinclair 1994). Another, more extreme specialisation in seen in the klipspringer (*Oreotragus oreotragus*), a browser specifically adapted to life on steep, rocky hilltop terrain and kopjes across the Serengeti (Kingdon 1982a, 1997; East 1988; du Toit & Owen-Smith 1989; Hofmann 1989; Estes 1991; Roberts 1998; Plate 1f).

The Antilopini tribe, which branched off from their neotragine ancestors in the Miocene, adapted to subsist in areas too dry and poor to support larger roughage eaters (Kingdon 1997; Brashares *et al.* 2000). This tribe of medium-sized antelopes increased in abundance and species richness toward the end of the Pleistocene era, when conditions became more arid (Kingdon 1982b; Estes 1991; MacDonald 2001). Two species are present in the Serengeti, Thomson's gazelle (*Gazella thomsonii*) and Grant's gazelle (*Gazella granti*). Both are gregarious, wide-ranging gleaners, capable of inhabiting the dry open plains (Maloiy 1963; Dorst & Dandelot 1970; Kingdon 1982b; 1997; Sinclair 1983; East 1988; Hofmann 1989; Estes 1991; FitzGibbon 1994; Stuart & Stuart 1997; Plate 2a-b). Thomson's gazelle, the smaller of the two, has become highly successful at exploiting seasonal grassland productivity by dispersing over the plains during the wet season and migrating into the north during the dry season (Dorst & Dandelot 1970; Delany & Happold 1979; Kingdon 1982b, 1997; Estes 1991; Stuart & Stuart 1997; see section 1.5.4). Grant's gazelle, by comparison, has capitalised on its ability to subsist on the vegetation available in waterless, semi-desert conditions, concentrating its movements around the plains and woodland edges in both seasons (Maloiy 1963; Kindgon 1982b; Estes 1991). Unlike Thomson's gazelle, it is able to vary its diet in response to resource availability, feeding on sturdier herbs and shrub foliage during the dry season (Talbot & Talbot 1962; Spinage *et al.* 1980; Kingdon 1982b, 1997; Hofmann 1989; Estes 1991).

In contrast, the Reduncini tribe, consists of species closely associated with permanent sources of water (Brashares *et al.* 2000). For instance, fossil records show that by the Pleistocene the ancestors of the Bohor reedbuck (*Redunca redunca*) and defassa waterbuck (*Kobus ellipsiprymnus defassa*) had already adapted to lacustrine habitats (Sinclair 1979b; Plate 2c-d). These two species, specialising in the exploitation of edaphic plants in swamps, flood plains, and valley bottoms, continue to fill this niche within the Serengeti (Dorst & Dandelot 1970; Delany & Happold 1979; Henshaw 1979; Kingdon 1982a; 1997; Sinclair 1983; East 1988; Estes 1991; Stuart & Stuart 1997; Brashares *et al.* 2000).

The resident representatives of the Hippotragini (the horse antelopes) in the ecosystem, are the roan (*Hippotragus equinus*) and the fringe-eared oryx (*Oryx gazella callotis*) (East 1988; Plate 2e-f). The former is predominately a grazer of medium to tall grasslands, while the latter is a grazer of short grasslands (Henshaw 1979; Kingdon 1982b, 1997; Estes 1991; Stuart & Stuart 1997). However, its dependence on water restricts its distribution to the western corridor and northern extension (Kingdon 1982b). The Alcelaphines, on the other hand are the archetypical large, grazing, plains' antelope (Talbot & Talbot 1962; Sinclair 1983; Hofmann 1989; Brashares *et al.* 2000). By the beginning of the Pleistocene their ancestors were less water-dependent and consequently able to inhabit open grasslands (Sinclair 1979b). Of the three species of this tribe, currently in the Serengeti, wildebeest (*Connochaetes taurinus*) are by far the most abundant (Plate 3a) and like the Thomson's gazelle, they exploit seasonal grass productivity (Dorst & Dandelot 1970; Owaga 1975; Delany & Happold 1979; Kingdon 1982b, 1997; Walther 1995; Estes 1991; Stuart & Stuart 1997; see section 1.5.4). Coke's hartebeest (kongoni) (*Alcelaphus buselaphus cokii*), in contrast, is adapted to inhabit small woodland-surrounded grasslands and whistling thorn (*Acacia drepanolobium*) scrubland (East 1988; Plate 3b). Here, they selectively graze tall and medium perennial grasses, such as red-oat grass (Dorst & Dandelot 1970; Gosling 1974; Delany & Happold 1979; Kingdon 1982b, 1997;

Estes 1991; Stuart & Stuart 1997). The topi (*Damaliscus lunatus*), the smallest of the three, appears to occupy an intermediate niche, preferring to graze on more open floodplain grasslands (Dorst & Dandelot 1970; Jewell 1972; Delany & Happold 1979; Kingdon 1982b, 1997; Estes 1991; Stuart & Stuart 1997; Plate 3c).

The equivalent size-related browsing niche is filled by the Tragelaphini tribe, part of the Bovine subfamily (Brashares *et al.* 2000). Radiating from ancestral stock in the Pliocene, two species are now present in the Serengeti, the common (cape) eland (*Taurotragus oryx*) and the bushbuck (*Tragelaphus scriptus*), the smaller of the two (Kingdon 1997; Plate 3d-e). These antelopes are found in wooded habitats, adapted to gleaning a diet of soft, nutritious vegetation and fruit from trees, shrubs and leguminous herbs (Dorst & Dandelot 1970; Delany & Happold 1979; Okiria 1980; Kingdon 1982a; Sinclair 1983; East 1988; Hofmann 1989; Estes 1991; Stuart & Stuart 1997). Eland are nomadic in response to the frequently ephemeral or scattered nature of soft browse (Briand Petersen & Casebeer 1971; Underwood 1981; Kindgon 1982a; Estes 1991). This behaviour is supported by their broad habitat tolerance and ability to consume a wide variety of dicotyledonous material (Kingdon 1982a, 1997). The bushbuck, on the other hand, is a forest edge dweller, essentially dependent on thick cover predominately near watercourses (Okiria 1980; Kingdon 1982a; 1997; du Toit & Owen-Smith 1989; Estes 1991; Stuart & Stuart 1997).

Also in Bovine subfamily is the tribe Bovini, that includes some of the most advanced ruminants to have evolved during the latter part of the Pliocene (Estes 1991; Brashares *et al.* 2000; MacDonald 2001). With a wide incisor row and massive molars, able to harvest and grind course grasses in large quantities, they are very specialised large grazers (Leuthold 1972; Sinclair 1974; Kingdon 1982a, 1997; Hofmann 1989; Estes 1991). However, many buffalo (Bovini) species disappeared about 1 Mya leaving only one existing species, the African buffalo (*Syncerus caffer*) (Sinclair 1979b; Plate 3f). An explanation for this maybe that as aridity increased at this time, the water-dependent buffalo species were unable to compete with the more adaptable wildebeest (Sinclair 1974a). Consequently, the African buffalo is now restricted to wooded or forested regions of the Serengeti (Henshaw 1979; Sinclair 1973a, 1974a, 1983; Kingdon 1982a, 1997; Estes 1991; Stuart & Stuart 1997).

Finally, the impala (*Aepyceros melampus*), is the only existing member of the Aepycerotini tribe (Kingdon 1997; Brashares *et al.* 2000; Plate 4a). The ancestry of this medium sized antelope is still very unclear. Until recently it was believed to be closely related to the Antilopini and Reduncini tribes, now it is thought to have diverged from the Alcelaphini tribe (Kingdon 1982b, 1997; Sinclair 1983; Brashares *et al.* 2000). It is a mixed feeder, able to utilise both monocotyledons and dicotyledons (Talbot & Talbot 1962; Dorst & Dandelot 1970; Delany & Happold 1979; Dunham 1980a, b; Hofmann 1989; Estes 1991; Kingdon 1997; Stuart & Stuart 1997). Moreover, it has a particular preference for light woodland and fragmented grasslands with well-drained soils on moderate slopes (Schenkel 1966; Jarman 1976; Dunham 1980a; Murray 1982a; East 1988; Kingdom 1982b, 1997; Estes 1991).

1.5.2 Family Giraffidae

The highly adapted browsing ruminants of the Giraffidae family, are one of the earliest Artiodactyla to have evolved. They first appeared in the late Miocene, and gave rise to the modern day giraffe (*Giraffa camelopardalis*) during the Pliocene (Hofmann 1973, 1989; Chrucher 1978; Kingdon 1979, 1997; Simpson 1984; MacDonald 2001; Plate 4b). Their specialised anatomy and physiology, in particular their elongated neck and legs, allow giraffe to access a two-metre band of foliage beyond the reach of most herbivores (Mitchell 1966; Leuthold & Leuthold 1972; Delany & Happold 1979; Pellew 1984; du Toit 1990; Woolnough & du Toit 2001). They are also adapted to combat tree defences. Horny papillae protect their lips and tongue against thorns, while a narrow muzzle, extremely flexible upper lip and a long prehensile tongue, allows giraffe to strip leaves off branches or select leaflets from between thorns (Estes 1991). Hence, Maasai giraffe (*G. camelopardalis tippelskirchi*) are able to feed on more or less every tree species in the Serengeti (Dagg 1960; Dorst & Dandelot 1970; Dagg & Foster 1976; Delany & Happold 1979; Leuthold & Leuthold 1972; Estes 1991; Stuart & Stuart 1997).

1.5.3 Non-ruminant Artiodactyla

There are two non-ruminant families within the order Artiodactyla, the Suindae and Hippopotamidae, whose common ancestors diverged in the late Eocene (Kingdon 1979, 1997; MacDonald 2001). However, it was not until the Oligocene they became distinguishable. The widespread Hippopotamidae ancestor of the time, Anthracotheriidae, was still a large pig-like herbivore (Owen-Smith 1988). By the lower Miocene, fossil records indicate that this family were already favouring semi-aquatic habitats and by the Pliocene, two coexisting species of true hippopotamus appeared in Africa, *Hippopotamus gorgops* and the present day, *H. amphibius* (Owen-Smith 1988). Speciation continued into the Pleistocene, giving rise to at least six more species (Kingdon 1979, 1997). Kenya's Lake

Turkana, for example, supported no less than four species at this time (Kingdon 1979, 1997; Estes 1991). *H. amphibius* is now one of two surviving species in Africa and the only species to reside in a number of the Serengeti's water sources (Olivier & Laurie 1974; Karstad & Hudson 1984; Simpson 1984; Owen-Smith 1988; Wolanski & Gereta 1999; Plate 4c). As a grazer, the hippopotamus has also evolved specialised wide muscular lips, enabling it to graze a broad swath, even in short grasslands (Kingdon 1979, 1997; Estes 1991; Stuart & Stuart 1997).

The other non-ruminant family is the Suindae, consisting of well-adapted rooting omnivores (Kingdon 1997). This formerly rich family lost at least a dozen African species in the late Pleistocene (Estes 1991; Kingdon 1997; MacDonald 2001). Those that have survived and persist in the Serengeti include the bushpig (*Potamochoerus larvatus*), a nocturnal woodland dweller from the subfamily Suinae, and the common warthog (*Phacochoerus africanus*), an open grassland inhabitant (Dorst & Dandelot 1970; Breytenbach 1979; Delany & Happold 1979; Henshaw 1979; Kingdon 1979, 1997; Estes 1991; Stuart & Stuart 1997; IEA 1999; Plate 4d-e). The latter evolved in Africa from a divergent line that arose in the Miocene, and is a predominantly grazing herbivore (Kingdon 1979, 1997; Estes 1991).

1.5.4 Perissodactyla

The Serengeti-Mara has only two representative species from the Perissodactyla order, the black rhinoceros (*Diceros bicornis*), a member of the Rhinocerotidae, and the plains or Burchell's zebra (*Equus burchellii*), belonging to the Equidae (Hack *et al.* 2002; Plates 4f & 5a). Fossil records show that the first true rhinoceros evolved from a small tapir-like Asian ancestor during the Eocene (Kingdon 1979, 1997). Between the Miocene and Pliocene, the family had reached its peak diversity with over 30 different genera present throughout Eurasia, North America and Africa (Estes 1991; MacDonald 2001). It was at this time that the ancestors of the modern rhinoceros first appeared as members of the genus *Paradiceros* (Owen-Smith 1988). By the early Pliocene this had given rise to the genus *Diceros*, from within which the only remaining Serengeti representative of the Rhinocerotidae, the black rhinoceros (*Diceros bicornis*) evolved. As a generalist browsing mega-herbivore, its niche includes shrub and woodland habitats (Ritchie 1963; Mitchell 1966; de Vos 1969; Mukinya 1973; Frame 1980; Carter 1984; Owen-Smith 1992; Estes 1991; Oloo *et al.* 1994; Kingdon 1997; Stuart & Stuart 1997).

Equidae have a similar evolutionary history with the first evolving from *Hyracotherium* (formerly *Eohippus*, the 'dawn-horse'), a small duiker-like forest animal in North America (Estes 1991; Kingdon 1997; Oakenfull & Ryder 2002). By the time *Equus* appeared in the early Pleistocene (2 Mya), some 20 other genera had already successfully spread into Eurasia and Africa until their dominance was usurped by ruminants in the late Miocene (Kingdon 1979, 1997; Owen-Smith 1992; Estes 1991; MacDonald 2001). *Equus* is now the only extant Equidae genera, with 6 existing species adapted to life on prairies, plains and steppes (Kingdon 1979, 1997; Estes 1991; Hack *et al.* 2002; Oakenfull & Ryder 2002). Burchell's zebra, one of four African equids, is one of the more successful Serengeti herbivores. Like the wildebeest and Thomson's gazelle, it has adopted a large-scale migratory strategy, exploiting seasonal productivity (Dorst & Dandelot 1970; Delany & Happold 1979; Owaga 1975; Kingdon 1979, 1997; Stuart & Stuart 1997; Hack *et al.* 2002).

Evidence suggests that this strategy arose nearly 1 Mya, during which time climate fluctuations became seasonal (Watson 1966; Aidley 1981). Its continuation indicates that the Serengeti climate has remained relatively constant ever since. Of course, this migratory behaviour is just another form of 'foraging optimisation', as exhibited by all herbivores (Leuthold 1972; Hillman 1988; Fryxell & Sinclair 1988b; Rodgers & Swai 1988; Kgathi & Kalikawe 1993; Gichohi *et al.* 1996; Drent & van der Wal 1999). Such strategies, developed during the coevolution with plants, were adopted to maximise net intake and were primarily defined by plant characteristics (Drent & van der Wal 1999). For example, a herbivore's demand for food can not exceed its resource's growth rate. This forces a herbivore to move away from an area it has exhausted into another more favourable area (Fryxell & Sinclair 1988b; Fryxell 1995). However, this movement can be restricted by certain factors. For instance, patchy habitats and resources both influence the extent and direction of herbivore movements (Fryxell 1995). Some herbivores are also dependent on other resources, such as water. Their movements will therefore be restricted around that particular resource, as seen in waterbuck, bushbuck, reedbuck and even impala (Spinage 1969; Young 1972; Waser 1975; Kingdon 1982a, 1997; Estes 1991). A consequence of these factors is that all herbivores generally have cyclic movements (Spinage 1969; Leuthold 1972; Owen-Smith 1977; McNaughton 1979b; Pennycuick 1979; Fryxell & Sinclair 1988a; Hillman 1988; Fryxell 1995; McNaughton & Banyikwa 1995; Mulder & Harmsen 1995; Prins 1996; Drent & van der Wal 1999). However, the time it takes a herbivore to return specific area depends on a further three factors, regrowth, senescence and grazing intensity (Sinclair 1974a; Vesey-FitzGerald 1974; Fryxell 1995; McNaughton & Banyikwa 1995; McNaughton *et al.* 1997a Drent & van der Wal 1999).

These in turn define the size of the area in which these cyclic movements occur, often referred to as home ranges (Jewell 1966; Leuthold 1972; Walther 1972; Hillman 1988).

Of course, the cyclic movements of some wildebeest, zebra and Thomson's gazelle across the Serengeti appear to be extreme in comparison to other herbivores in the area. One possible explanation is that prior to the arrival of seasons, each species had two fairly separate populations between which transfer was virtually non-existent. One had taken up residence in the more wooded regions of the western corridor and northern extension, while the other had adjusted its foraging strategy to suit the open grassland habitat of the plains (Onyeanusi 1989). As climate gradually changed and grass production began to decrease at certain times of the year, the plains populations progressively extended their range into the north from the plains (Watson 1966; Pennycuick 1975; Western 1975; Walker & Noy-Meir 1982; Fryxell *et al.* 1988; McNaughton & Banyikwa 1995; Wolanski *et al.* 1999; see section 3.3.5). Here, physiographical differences created a wetter environment and subsequently enabled vegetation to grow for most of the year (McNaughton 1989). Despite this, the soils in the area are dystrophic (lacking nutrient) and its grasses tend to fibrous and provide little mineral content, making them less nutritious and less digestible (Bell 1971; Braun 1973; Kreulen 1975; van Soest 1982; Fryxell & Sinclair 1988a; Fryxell *et al.* 1988; Gichohi *et al.* 1996). By returning to the plains when grass becomes abundant again, grazers benefit from the area's higher quality grasslands, increasing population growth rates through reduced mortality and increased reproduction (Watson 1967; McNaughton 1985; Fryxell & Sinclair 1988a; Fryxell 1995). Those herbivore species that have populations whose cyclic movements extend from the plains to the surrounding area (migrants) can, therefore, maintain high population numbers (Kreulen 1975; Maddock 1979; Aidley 1981; McNaughton 1984; Fryxell & Sinclair 1988a, b; Wolanski *et al.* 1999; Serneels & Lambin 2001). For example, the plains wildebeest population now consists of over a million animals, while the zebra and Thomson's gazelle populations reach hundreds of thousands (Estes 1966; Hilborn & Mangel 1997).

The mass migration of these populations is now a characteristic feature of the Serengeti-Mara ecosystem (Watson 1967; Herlocker 1975; Fryxell & Sinclair 1988b; Gichohi *et al.* 1996; Murray 1995; Wolanski *et al.* 1999). In fact, when the area was recognised to have conservation potential, such movements determined the initial region chosen, subsequent additions and final boundary demarcation (Pearsall 1957; Grzimek & Grzimek 1960; Talbot & Talbot 1963; Watson 1967; Pennycuick 1975; McNaughton 1985; McNaughton & Banyikwa 1995). In contrast, many reserves established over the last 50 years, had little concern for, or knowledge of, the spatial movements of the animals they were designed to preserve (Laws *et al.* 1975; Western & Ssemakula 1981). The Serengeti now constitutes a well-defined functional unit and consequently has maintained much of its integrity over the years (Wolanski *et al.* 1999; Rodgers & Swai 1988; Talbot & Talbot 1963; Noss & Csuti 1997).

1.5.5 Proboscidea

The Proboscidea first appeared in Africa during the late Miocene as *Primelephas*, the earliest recognised elephant (Douglas-Hamilton 1980; Owen-Smith 1992; MacDonald 2001). This eventually gave rise to the exclusively African genus, *Loxodonta,* in the late Pliocene, from which the modern day elephant *L. africana* evolved (Douglas-Hamilton 1980; Owen-Smith 1992; Plate 5b). However, this species did not appear on savannahs until the late Pleistocene, as prior to this it was restricted to forested habitats. The elephant is currently the largest mammal (mega-herbivore) in the Serengeti-Mara ecosystem, weighing an average 4,300 kg (Dorst & Dandelot 1970; Delany & Happold 1979; Kingdon 1979, 1997; Damuth 1987; Estes 1991; Stuart & Stuart 1997). This hindgut fermenter is a mixed feeder and, as such, has intermediate physiological characteristics (Clemens & Malioy 1982; Laws 1966; Maglio 1973; McNaughton & Georgiadis 1986; Owen-Smith 1992; Kabigumila 1993). Its dentition leans towards that of a grazer with its high-crowned molars, but the presence of folds in the enamel of these molars creates numerous plates capable of grinding both grasses and dicotyledonous browse (Owen-Smith 1992; Kalemera 1989; Kabigumila 1993, Spinage 1994). Its prehensile trunk, a modified nasal region, enables the elephant to gather a wide variety of grasses from floor level, as well as leaves above its head (Delany & Happold 1979; Kingdon 1997; Stuart & Stuart 1997). This generalist feeding behaviour allows it to forage on most available vegetation at any one time.

1.5.6 Other Ungulata

Tubulidentata was the first Subungulata order to diverge early in the Palaeocene from the earliest ungulate ancestor, the Condylarthra (Melton 1976; Jones 1984; Wilson & Reeder 1993; Kingdon 1997; MacDonald 2001). Initially, its species were thought to closely resemble anteaters, in the order Edentata, but relatively recent studies into their physiology has revealed that they are unrelated (Melton 1976; Jones 1984; Wilson & Reeder 1993; MacDonald 2001). Although both groups are specialised termite and ant eaters, anteaters are truly toothless, where as Tubulidentata species have peg-like molars and premolars formed from columns of dentine (Melton 1976; Jones 1984). However, the only extant member of this order is the aardvark (*Orycteropus afer*), a nocturnal, secretive, pig-like animal with a long, sticky tongue and well developed salivary glands adapted to aid the capture of its insect prey (Melton 1976; Bourlière 1983; Estes 1991; Kingdon 1997; Plate 5c).

Another primitive offshoot from the Condylarthra gave rise to the Hyracoidea in Africa during the Palaeocene (Kingdon 1979, 1997; Wilson & Reeder 1993; MacDonald 2001). Like the closely related Proboscidea, the Hyracoidea became both widespread and diverse about 40 Mya (Hoeck 1984; Jones 1984). The order then declined during the Miocene (25 Mya), perhaps due to an inability to compete with the now prolific Artiodactyla. Today, this order is confined to Africa and the Middle East, and within the Serengeti there are only two representative species, the rock (Jonston's) hyrax (*Procavia johnstoni*) and the bush (Bruce's yellow-spotted) hyrax (*Heterohyrax brucei*) (Turner & Watson 1965b; Dorst & Dandelot 1970; Kingdon 1979, 1997; Olds & Shoshani 1982; Stuart & Stuart 1997; Gerlach & Hoeck 2001; Plate 5d-e). The distribution of both species is patchy as they are restricted to rocky outcrops, where they feed on a wide variety of plants, grasses, fruits and berries (Turner & Watson 1965b; Hoeck 1975, 1982; Hoeck *et al.* 1982; Estes 1991; Malioy & Eley 1992; Kingdon 1997; Gerlach & Hoeck 2001).

1.5.7 Carnivora

All modern carnivores arose from an insectivorous ancestor some 65 Mya (Kingdon 1977, 1997; Estes 1991; MacDonald 2001). The earliest carnivorous mammals belonged to an archaic order, the Creodonta (flesh-tooth; Estes 1991). As herbivores diversified, only one family of Creodonts was able to do the same, the small, weasel-like arboreal miacids and it is from these that all modern carnivores are believed to be descended (Kingdon 1977, 1997; Martin 1989; Estes 1991; MacDonald 2001). By the end of the Oligocene, all but two of the existing Carnivora families had arisen, coinciding with the extensive speciation of Artiodactyla, Perissodactyla and Rodentia (Slobodkin 1974; Martin 1989; Estes 1991). Two superfamilies diverged early on in the Carnivora's adaptive radiation, the Canoidae and Feloidae (Estes 1991). Within the latter group, two families emerged during the late Eocene, the Viverridae and Felidae. The former is considered to be physically and behaviourally similar to their miacid ancestors. In the Serengeti three Viverridae subfamilies exist, the Viverrinae, Paradoxurinae and Herpestinae. The African civet (*Civettictis civetta*) is one of two Viverrinae present (Plate 5f). This arboreal, omnivorous, dog-like animal has adapted a tolerance to eating the more poisonous or distasteful plants and animals in the area (Dorst & Dandelot 1970; Estes 1991; Kingdon 1997; Stuart & Stuart 1997). Its closest living relative, the common (European or small-spotted) genet (*Genetta genetta*), has a more general diet within the arboreal niche (Kingdon 1977, 1997; Bourlière 1983; Estes 1991; Stuart & Stuart 1997; Plate 6a). A niche also filled by the local Paradoxurinae species, the African palm (tree) civet (*Nandinia binotata*) (Bourlière 1983; Plate 6b). By contrast, the subfamily Herpestinae are carnivorous and extremely diverse. Within the Serengeti there are six species, each with specific diet and habitat requirements (Dorst & Dandelot 1970; Neal 1970; Kingdon 1977, 1997; Bourlière 1983; Estes 1991; Creel 1996a; Stuart & Stuart 1997). These are the marsh mongoose (*Atilax paludinosus*), the Egyptian (grey) mongoose (*Herpestes ichneumon*), the slender (black-tipped) mongoose (*Herpestes sanguineus*), the dwarf mongoose (*Helogale parvula*), the banded mongoose (*Mungos mungo*) and the white-tailed mongoose (*Ichneumia albicauda*) (Neal 1970; Waser 1980; IEA 1999; Plates 6c-f & 7a-b).

The third family, the Felidae, contains the most specialised carnivorous hunters. The first recognisable felids appeared 40 Mya and ancestors of extant cats were present by 24 Mya (MacDonald 2001). The most notorious of these ancestors was the saber-toothed cat, considered to be related directly to the genus *Panthera*, two species of which still inhabit the Serengeti. One of these is the lion (*Panthera leo*), found on the open grasslands and in open woodland (Adamson 1964; Dorst & Dandelot 1970; Kingdon 1977, 1997; Bourlière 1983; Estes 1991; IEA 1999; Plate 7c). This large, muscular cat hunts in social groups or prides, preferring to prey on the larger herbivores, particularly the migratory species (Kruuk & Turner 1967; Elliott *et al.* 1977; Kingdon 1979, 1997; Lamprecht 1981; Estes 1991; Nowell & Jackson 1996). These prides form the core units of a matrilocal society, consisting of a number of related females and their cubs (Bertram 1976; Kingdon 1977; Giraldeau & Gillis 1988; Packer *et al.* 1990; Nowell & Jackson 1996). Throughout the year, each pride holds a permanent territory, covering a home range that may have been passed down through generations (Giraldeau & Gillis 1988; Packer *et al.* 1990; Nowell & Jackson 1996). In contrast, the leopard (*Panthera pardus*) is a nocturnal, solitary cat adapted for life in the Serengeti woodlands (Bertram 1982; Dorst & Dandelot 1970; Bourlière 1983; Estes 1991; Kingdon 1997; IEA 1999; Plate 7d). It is well known for its versatility as a generalist predator, possessing a number of morphological adaptations enabling it to hunt in its preferred habitat (Kruuk & Turner 1967; Kingdon 1977; Estes 1991; Nowell & Jackson 1996). Its whiskers are particularly long, assisting movement through vegetation in darkness and the presence of several long hairs in its eyebrows protect its eyes (Skinner & Smithers 1990). It uses agility, stealth and the element of surprise to capture its prey whether it is an eland or a dung beetle. Its broad diet allows the leopard to adapt quickly to changes in prey availability (Nowell & Jackson 1996).

Another 'big cat' of the Serengeti is the cheetah (*Acinonyx jubatus*) (Bourlière 1983; IEA 1999; Plate 7e). Like the lion, it inhabits open grasslands, such as the plains (Schaller 1968; Caro & Collins 1986). In contrast, it is a nomadic, solitary, cursorial hunter (Kruuk & Turner 1967; Schaller 1968; Dorst & Dandelot 1970; Kindgon 1979, 1997; Lamprecht 1981; Caro & Collins 1986; Estes 1991; Nowell & Jackson 1996; Stuart & Stuart 1997). Other smaller felids include the true cats (*Felis*) that appeared in South Africa during the Pliocene. In the Serengeti, the caracal (*Felis caracal*), a relatively small predator, inhabits the *Acacia* and *Commiphora* woodlands and thickets (Dorst & Dandelot 1970; Kingdon 1979, 1997; Waser 1980; Estes 1991; Wilson & Reeder 1993; Nowell & Jackson 1996; Stuart & Stuart 1997; Plate 7f). The African wild (kaffir) cat (*Felis silvestris lybica*) inhabits a wide ecological range throughout the ecosystem, considered to be a consequence of its ability to subsist on insects and yet take mammalian prey of its own size (Dorst & Dandelot 1970; Kingdon 1979, 1997; Estes 1991; IEA 1999; Plate 8a). Finally, the serval (*Felis serval*), is adapted, with its relatively long legs and tall vertically set ears, to hunt efficiently for small animals in tall grass, its preferred habitat (Dorst & Dandelot 1970; Kingdon 1977, 1997; Estes 1991; Stuart & Stuart 1997; Newman 1998; Plate 8b).

The family Canidae has existed for some 55 million years (MacDonald 2001). It originated in North America and soon diversified and spread to Eurasia and African. There are 5 species, within three separate genera, present in the Serengeti. The bat-eared fox (*Otocyon megalotis*) is believed to be from the most primitive genus and like the aardvark, has become a specialised insectivore (Koop & Velimirou 1982; Estes 1991; Plate 8c). Its ears are adapted to locate subterranean insects by sound, its fur is dense to protect it from insect bites and stings and it has a specialised dentition for breaking up hard-shelled insects (Kingdon 1977, 1997; Waser 1980; Koop & Velimirou 1982; Estes 1991).

Within the genus *Canis*, three omnivorous species occur in the Serengeti. These are the golden (common) jackal (*Canis aureus*), side-striped jackal (*Canis adustus*) and black-backed jackal (*Canis mesomelas*) (Kingdon 1977; Moehlman 1996; IEA 1999; Plate 8d-e). The former is adapted to subsist in arid areas and thus can reside on the plains year round (Kingdon 1977, 1997; Estes 1991). The side-striped jackal has great dietary flexibility and occupies many different habitats, while the black-backed jackal is closely associated with *Acacia* habitats and prefers a diet primarily of small mammals and carrion (Grafton 1965; Rowe-Rowe 1976; Kingdon 1977, 1997; Lamprecht 1978, 1981; Moehlman 1979, 1983, 1996; Estes 1991; Stuart & Stuart 1997).

Finally, there is the African hunting (wild) dog (*Lycaon pictus*) (Plate 9a). This species is the only member of the genus *Lycaon,* a unique lineage within the canids (Wozencraft 1989; Girman & Wayne 1997; MacDonald 2001). Unfortunately, in 1991 it became locally extinct in the Serengeti region due to a combination of human activites, disease and competition with other carnivores (Ammann 1987; Fanshawe *et al.* 1991; Sheldon 1992; Burrows *et al.* 1994, 1995; Creel *et al.* 1995; Ginsberg *et al.* 1995; van Heerden *et al.* 1995; Creel 1996b; Creel & Creel 1996; Dye 1996; East & Hofer 1996; Woodroffe & Ginsberg 1997, 1999; Durant 1998; Creel 2001; Scott & Scott 2001). They are the most social of the canids and, like the cheetah, are cursorial hunters cooperatively catching their prey by outrunning them (Kruuk & Turner 1967; van Lawick-Goodall & van Lawick-Goodall 1970; Malcolm & van Lawick 1975; Kingdon 1977, 1997; Frame *et al.* 1979; Lamprecht 1981; Estes 1991; Sheldon 1992; Moehlman 1996; Creel 1997; Stuart & Stuart 1997).

There are two further families within the Carnivora, the Mustelidae, considered to be primitive group and the Hyaenidae, the most recent to have evolved (MacDonald 2001). The mustelid branch diverged from the Carnivora in the Oligocene (Anderson 1989). It went through major adaptive radiations during the middle to late Tertiary period, although the earliest fossil records found in Africa date only from the middle Pliocene (Martin 1989; Estes 1991). Modern species from this family are considered to closely resemble the original carnivorous miacids in that they were ground and tree-climbing predators (Estes 1991). In the Serengeti, five Mustelidae species exist, occupying habitats and niches not filled by the Viverridae (IEA 1999). For instance, the Cape clawless otter (*Aonyx capensis*) and Spot-necked otter (*Lutra maculicollis*) are both aquatic vertebrate predators (Plate 9b-c). The honey badger (ratel) (*Mellivora capensis*) is a particularly opportunistic omnivore, but is morphological adapted to extract subterranean food (Waser 1980; Bourlière 1983; Nowak 1995; Plate 9d). It preys particularly on the nests of colonial insects, such as termites, ants and bees (Dorst & Dandelot 1970; Estes 1991; Kingdon 1997; Stuart & Stuart 1997). In fact, the honey badger is one of the few mammalian predators of bees, feeding on both larvae and honey (Estes 1991; Nowak 1995), hence its name *Mellivora*, meaning ‘honey eater’. The two other mustelids are the zorilla (striped polecat) (*Ictonyx striatus*) and the African striped (white-naped) weasel (*Poecilogale albinucha*), both commonly found on grasslands, preying primarily on invertebrates and rodents, respectively (Bourlière 1983; Plate 9e-f).

Fossil records show that the smallest and most recent carnivore family, the Hyaenidae, arose from the civets (*Progenetta*) around the late Miocene (10 Mya) (Estes 1991; Werdelin & Solounias 1991; Jenks & Werdelin 1998; MacDonald 2001). By the early

Pliocene they already resembled modern species, three of which reside in the Serengeti (IEA 1999). The striped hyaena (*Hyaena hyaena*), found commonly in *Acacia* scrub, is primarily an opportunist omnivorous scavenger (Kruuk 1976; Kingdon 1977, 1997; Bourlière 1983; Estes 1991; Stuart & Stuart 1997, Plate 10a). The spotted hyaena (*Crocuta crocuta*), one of the most abundant carnivores, is both a well-adapted scavenger and predator of mammals (Kruuk 1969; Dorst & Dandelot 1970; Kingdon 1977, 1997; Lamprecht 1981; Estes 1991; Hofer *et al.* 1993; Stuart & Stuart 1997; Plate 10b). It is able, like the striped hyaena, to crush and digest bones, but it has also adapted behaviourally to recognise vulnerability in its prey allowing it hunt almost any sized animal (Sutcliffe 1970; Kingdon 1977, 1997; Bourlière 1983; Estes 1991). The third hyaenid found in the Serengeti, is the aardwolf (*Proteles cristatus*) from the subfamily Protelinae (Kruuk & Sands 1972; Waser 1980; Plate 10c). This species superficially resembles the striped hyaena, although its physiology, particularly its dentition and digestion are specially adapted, like that of the aardvark, to feed exclusively on termites (Kingdon 1977, 1997; Estes 1991).

There are six other mammalian orders (Primates, Chiroptera, Insectivora, Lagomorpha and Rodentia) and many avian orders found in the Serengeti-Mara (Kingdon 1997; Stuart & Stuart 1997; Keesing 1998, 2002). Each is represented in the region by numerous species, all of which interact to a certain degree to influence each other's population dynamics. Together, the Serengeti fauna's combined inter-relationships make up a complex ecosystem.

1.6 Future conservation

If the Serengeti-Mara ecosystem is to retain its diverse and abundant fauna, more efficient long-term conservation is needed. By piecing together various aspects of the research carried out in the Serengeti-Mara, an understanding of how this ecosystem functions can hopefully be acquired. Based on this understanding, advise on appropriate conservation efforts can then be formulated. Creating a simulation model using available research data may well provide a way to achieve this. The next chapter, therefore, examines the role of models in ecology, while the preceding chapters describe the construction of a model simulating the Serengeti-Mara ecosystem and then discuss the application of this model as an analytical tool.

CHAPTER 2: MODELLING

2.1 INTRODUCTION

The development and use of models has become increasing popular in biology since the Lotka-Volterra competition model was proposed by Lotka (1925) and independently by Volterra (1926). Models are simplified representations of biological processes or structures, intended to facilitate prediction, calculation and understanding (Levins 1966; Skellam 1973; Starfield & Bleloch 1986; Brown & Rothery 1993; Keddy 2001; Lindenmayer *et al.* 2003). They can be mathematical models, such as equations or graphs, diagrammatic models, such as flow charts, or physical models, like model organs and the like, often seen in museums. There are now numerous examples of where different types of models have been used throughout many different branches of biology. Moreover, many of these have led to significant revelations in certain fields of science, such as the discovery of the structure of DNA by Watson & Crick through the construction of the double helix molecule with paper and pins (Watson & Crick 1953; Watson 1981). In medical science, modelling the spread of HIV/AIDS and malaria virulence have been, and still are, crucial in projecting the transmission of these diseases, raising awareness and influencing the implementation of preventative measures (Anderson & May 1987; Janssen & Martens 1996; Greenhalgh & Hay 1997; Garnett *et al.* 2002; Read 2002). In agriculture, models predicting crop growth and development are proving to be a highly sought-after tool (Dirks & Lantinga 1993).

In ecology, mathematically modelling a process, or a system, is now common practice. Such models shape the way in which questions are asked, help determine the amount and kind of data to be collected and force ecologists to state their assumptions (Starfield & Bleloch 1986; Brown & Rothery 1993; Lindenmayer *et al.* 2003). This chapter discusses various types of models that have been developed in ecology, particularly for conservation, and examines the most appropriate model required to represent an ecosystem, such as the Serengeti-Mara.

2.2 TYPES OF MATHEMATICAL MODELS

In their simplest form, mathematical models can be an equation showing how the magnitude of one variable can be calculated from others. With two or more equations, patterns between components can be identified, such as the growth and decline of populations (Walker *et al.* 1981; Brown & Rothery 1993). In fact, a wide range of different types of mathematical models can be used for all sorts of inquires. At one extreme there are empirical/descriptive models and at the other end, mechanistic/simulation models (Starfield & Bleloch 1986; Brown & Rothery 1993; Walker & Crout 1997). Simulation models are concerned with the mechanics of biological processes and the way in which the component parts fit together (Starfield & Bleloch 1986; Boyce 1992b; Keddy 2001). For example, Sinclair (1973b) applied this approach to a population of East Africa buffalo, from which he identified a population equilibrium, the processes that led to this equilibrium and the key factors that could potentially disturb the population. In contrast, descriptive models simply describe how one feature varies in relation to others without attempting to describe the underlying mechanics involved (Starfield & Bleloch 1986; Brown & Rothery 1993; Walker & Crout 1997; Keddy 2001). For example, a growth curve created through census data alone would be a descriptive model, while a mechanistic approach would include separate components contributing to the overall population change, such as birth and death rates (Brown & Rothery 1993; Stewart & Hutchings 1996).

Brown & Rothery (1993) state that both these types of model can be either dynamic, describing processes unfolding in time, or non-dynamic, representing a static relationship in a fixed time period. Both model types may also involve stochastic and deterministic components. A purely stochastic model enables us to predict the probability of a random event occurring or a series of events (Brown & Rothery 1993; Stewart & Hutchings 1996). For example, this type of model is frequently employed to predict genetic drift within a population (Caballero & Toro 2002; Souza *et al.* 2002; van Rossum *et al.* 2002; Elliott & Reilly 2003). In comparison, a deterministic model predicts the outcome following a random phenomenon, such as the resulting population size or genetic difference (Brown & Rothery 1993; Stewart & Hutchings 1996). Of course, many models may actually have a combination of both these factors. For instance, a stochastic model may have a deterministic component (reflecting a trend) within it or vice versa (Brown & Rothery 1993). Such an amalgam is a common feature of statistical models. For example, in a simple linear regression equation, $y = \mathrm{a} + \mathrm{b}x + \varepsilon$, x is the mean outcome, and therefore the deterministic element. However, as there is variation (ε) around this mean, there is a distribution of other probable outcomes and this is the stochastic element.

As models become increasing complex, consisting of a series of mathematical equations describing various processes acting in conjunction with one another, it becomes more difficult, if not impossible, to construct algebraic models by formal mathematical methods. (Boyce 1992b; Walker & Crout 1997). However, there is an alternative and that is to generate a model in a computer. Using a computer program eliminates the technical details more formal mathematical methods would become embroiled in (Brown & Rothery 1993). Quite simply, it performs the mathematics more directly within a short space of time. Once a simulation is set-up to follow specific criteria, it can be run repetitively using various starting parameters (Meffe *et al.* 1997). Brown & Rothery (1993) state that computer programs also allow a degree of parameter estimation, as it is easier to test them through a sensitivity analysis. This enables a modeller to determine whether an over- or underestimate of a variable may affect the outcome dramatically, rendering the model less useful. By successively adjusting a parameter, the degree to which the outcome changes can be assessed (Brown & Rothery 1993). If this change is small, the margin of uncertainty surrounding that parameter may not significantly affect the results. On the other hand, a large difference in outcome suggests the parameter needs to be measured more accurately as even small deviations have a large influence on the model's outcome. Furthermore, by using a computer, two or more parameters can be adjusted at a time, in order to assess whether a particular parameter only becomes critical in conjunction with other parameters (Meffe *et al.* 1997). This in turn allows a more intuitive understanding of a process or system to be gained (Brown & Rothery 1993). The use of computer modelling has consequently opened a number of avenues of study that would otherwise remain impossible to model, particularly in the field of conservation (Meffe *et al.* 1997).

2.2.1 Modelling in conservation biology

It has become increasingly apparent that conserving a population requires an understanding of the links between demographic processes, such as birth, death, immigration and emigration, as well as the environment in which the population exists. Computer modelling has rendered this less of a challenge for conservation biologists and, as methods of conservation have evolved, so has the complexity of the required models. The first models of practical significance to conservation tended to explore basic species interactions, such as competition, predation and parasitism (Brown & Rothery 1993; Keddy 2001). For instance, the Lotka-Volterra competition model, simulates the competitive effect of one species on the growth rate of another (Lotka 1925; Volterra 1926). From this model, it is possible to predict population dynamics by varying the strength of competition by adjusting the competition coefficient (α) and/or carrying capacity (K), or disclosing the strength of the competition by inputting specific population data. Lotka-Volterra competition models have served as a foundation for the construction of other models (Simberloff 1983; Fagerstrom 1987; Keddy 2001). Initially these explored single processes such as predator-prey and host-parasitoid interactions (Keddy 2001). They have since evolved, and many conservation biologists are now focusing on modelling whole ecological communities. Such models incorporate a matrix of *n* interacting species in a temporally and spatially varying environment (Keddy 2001). These have allowed the comparison of different species, and the exploration of responses to environmental/ecological perturbations (Pimm 1991; Krebs *et al.* 1999; Keddy 2001). For instance, once perturbed, a population may return to a stable state or may continue to diverge from it, either monotonically or through oscillations (Sinclair 1973b; May 1975; Pimm 1991). Moreover, perturbations are also very important when testing the accuracy of a model. If the model population responds to a perturbation in the same way as the equivalent natural population, the model would appear to be suitably describing the real population. Consequently, these models can then provide land managers with a new tool for predicting how management plans and land use changes may affect species/populations of concern (Pascual & Hilborn 1995; Pulliam & Dunning 1997; Crooks *et al.* 1998; Boone *et al.* 2002). For example, Mduma *et al.* (1998) modelled the effects of poaching on the Serengeti wildebeest population and were able to investigate the potential for this population to be legally harvested.

Out of the many models that have been developed for conservation purposes, perhaps the most comprehensive modelling approach is Population Viability Analysis (PVA) (Young 1994; Stewart & Hutchings 1996; Pulliam & Dunning 1997; Boyce 2002; Frankham 2002). PVA is a branch of conservation biology that seeks to understand the relationship between species survival and habitat (Shaffer 1997). It recognises the importance of habitat type and its degree of suitability in determining overall population dynamics, such as abundance, fecundity or size (Young 1994). The roots of PVA can be traced back to MacArthur & Wilson's (1967) island biogeography theory, that attempts to explain the species diversity of island biotas. From their model it was proposed that the number of species on an island, at anyone time, represented a balance between the rate of immigration to the island and the rate of extinction (Soulé & Wilcox 1980; East 1981, 1983; Shaffer 1981; Gilpin & Soulé 1986; Shaffer 1997). It is from this model that the first principle of PVA was formulated.

Although PVA is a relatively new approach, a number of excellent studies have demonstrated its usefulness. At its most simplistic, PVA attempts to estimate the probability that a population will survive for a given number of generations (Stewart & Hutchings 1996; Pulliam & Dunning 1997). Metapopulation models also fall within this category. These are models that address the dynamics of population networks, where colonisation, extinction and dispersal are critical factors (Hanski & Gilpin 1997). These have been successfully used to study the dynamics of the threatened bay checkerspot butterfly (*Euphydryas editha bayensis*) and the bog fritillary butterfly (*Proclossiana eunomia*) (Murphy *et al.* 1990; Sawchik *et al.* 2002). Such models are useful for gaining general insights into population dynamics when there is demographic and environmental stochasticity (such as changes in weather, food supply and the populations of competitors), and influences from predators, parasites, and natural catastrophes. These factors may contribute to the increased probability that a population will become extinct (Soulé 1987; Shaffer 1990; Pulliam & Dunning 1997). In order to manage a particular species in a particular habitat, these models must incorporate specific spatial and behavioural data (Harrison 1991).

Spatially explicit models, such as cellular automata models, incorporate realistic details of particular species and landscapes, such as the dispersal behaviour of organisms among suitable habitat patches (Dytham 1994, 1995; Pulliam & Dunning 1997). One prevalent example of a spatially explicit computer model is the mobile animal population (MAP) model, which is created to represent actual landscapes (Pulliam *et al.* 1992; Liu 1993; Liu *et al.* 1995). It depicts the current landscape structure and predicts future dynamics within its specific configuration (Pulliam *et al.* 1995). Unfortunately, because such a model is so specific, the conclusions reached from it are not easily generalised to other species and landscapes. However, the use of MAP models has proven valuable in a variety of conservation management challenges, as in the case of the Bachman's sparrow (*Aimophila aestivalis*) (Liu *et al.* 1995). Here, a MAP model was used to determine whether forest management practises influenced the population viability of the sparrow in pine forests in the southeastern United States (Liu *et al.* 1995). Similar models have been constructed investigating the response of wintering elk (*Cervus elaphus*) and bison (*Bison bison*) herds to the effects of large-scale fires in Yellowstone National Park (Turner *et al.* 1994, Pearson *et al.* 1995), the suitability of central European landscapes for the reintroduction of Eurasian lynx (*Lynx lynx*) (Schadt *et al.* 2002) and the viability of the spotted owl (*Strix occidentalis*) in the Pacific northwest of the United States (Thomas *et al.* 1990; Verner *et al.* 1992; McKelvey *et al.* 1993).

Although, the application of PVA related models over the last decade has increased understanding of extinction dynamics (Boyce 1992a; Nantel *et al.* 1996; Shaffer 1997; Cross & Beissinger 2001; Araujo *et al.* 2002), they tend to be based on a individual high profile species. For example, the grizzly bear (*Ursus arctos horribilis*) in Yellowstone National Park (Shaffer 1983, 1990, 1997; Shaffer & Sampson 1985; Stewart & Hutchings 1996; Allendorf 1997), the Ethiopian wolf (*Canis simensis*) (Haydon *et al.* 2002), the endangered Carpentarian rock-rat (*Zyzomys palatalis*) in northern Australia (Brook *et al.* 2002) and the endangered Sonoran pronghorn (*Antilocapra americana sonoriensis*) in southwestern Arizona (Hosack *et al.* 2002) have all been studied using a PVA approach. This is not surprising, as a considerable amount of research is required to define relatively accurate parameters for these models. However, conservationists have increasingly recognised the need to conserve whole ecosystems, not just individual endangered species (May 1975; Holling 1978; Walker & Noy-Meir 1982; Baird Callicott 1997; Araujo *et al.* 2002). By focusing research on those species whose interactions are especially critical to the ecosystem, other species will be indirectly conserved as a result (Holling 1992; Power & Mills 1995; Power *et al.* 1996; Stewart & Hutchings 1996; Myers 1997; Shaffer 1997). It was Paine (1966) who first referred to those species whose removal, addition or fluctuation may have wide-ranging, cascading effects on other species, processes, interactions and even landforms, as 'drivers' or 'keystone' species (Paine 1969, 1995; Pimm 1991; Walker 1992). In contrast, 'passenger' species tend to have little influence on the structure of the ecosystem and are most likely dependent on the 'driver' species (Power & Mills 1995; Meffe *et al.* 1997).

A classic example of a keystone species, and the one for which the term was first coined, is the sea star *Pisaster ochraceus*, found in the rocky intertidal zone along the North American Pacific coast (Meffe *et al.* 1997). It was discovered that in the absence of *P. ochraceus*, the mussel (*Mytilus californianus*), one of the many invertebrate prey species of the sea star, became a dominant competitor, usurping large proportions of limited space. This led to a decrease in species richness, as a number of other rocky shore inhabitants were expelled (Paine 1966, 1969; Meffe *et al.* 1997). Consequently, *P. ochraceus* is believed to be 'keystone predator', along with the sea otter (*Enhydra lutris*) in rocky marine communities (Estes & Palmisano 1974; Krebs 1988; Kvitek & Oliver 1992; Kvitek *et al.* 1992), the blue crab (*Callinectes sapidus*) in estuarine seagrass beds (Cote *et al.* 2001), the stoneroller (*Campostoma anomalum*), a herbivorous minnow in the prairie streams of Oklahoma (Power & Matthews 1983; Power *et al.* 1985) and tiger sharks (*Galeocerdo cuvier*) in the nearshore ecosystems of Shark Bay, Western Australia (Heithaus 2001). These examples emphasise the direct and obvious impact that keystone species can have on an ecosystem.

However, indirect and more cryptic effects of these species, may be just as critical in ecosystem function. For instance, one salient feature of keystone predators is that their presence in a community can have far-reaching effects on species they do not consume (Meffe *et al.* 1997).

Other types of keystone species include 'keystone food resources' and 'habitat modifiers' or 'ecosystem engineers' (Meffe *et al.* 1997; Crooks 2002). Terborgh (1986) discovered that in the tropical forests of Central & South America, the nectar and fruits of certain plants, although representing less than 1 % of the plant diversity, sustained nearly the entire frugivore community through a three-month period each year. Terborgh (1986) concludes that such species represent 'keystone food resources' as their removal would result in ecosystem collapse. Another keystone food resource appears to be certain freshwater anadromous fish found to have critical influences on the social interactions, distribution, activity patterns and possibly survivorship of species within associated aquatic and terrestrial ecosystems (Wilson & Halupka 1995). On a similar note, Jones *et al.* (1994), refers to the beaver (*Castor canadensis*) as an 'ecosystem engineer', as they transform free-flowing streams into ponds and lakes, destroying large expanses of surrounding forest. These changes in the environment may affect habitat availability and structure for many terrestrial, aquatic and semi-aquatic species (Naiman *et al.* 1986; Wright *et al.* 2002). Similarly, pocket gophers (*Geomyidae spp.*) are considered to be ecosystem engineers, due to their profound impact on vegetation and soil composition within their habitat (Reichman & Seabloom 2002).

As keystone species play a central role in an ecosystem's processes, they tend to be a focal point in modelling an ecosystem (Fryxell *et al.* 1988; Holling 1992; Hofer *et al.* 1993; Western & Gichohi 1993; Homewood *et al.* 2001). However, models may need to represent an ecosystem more fully in order to make suitable management decisions. Gignoux *et al.* (1998) attempted to do this by creating a spatial model simulating function and dynamics surrounding all the primary producers in West African and Australian savannahs. A more recent model constructed by Boone *et al.* (2002) for the Ngorongoro Conservation Area, simulates the competitive interactions between a number of major wild herbivores and their domestic equivalents. Although it was designed to assess land-use between Maasai pastoralists and wildlife conservation, its successful construction at such a high level of complexity indicates that modelling in conservation is still advancing. The Serengeti-Mara ecosystem poses, at present, a unique opportunity to construct a model encapsulating the entire East African ecosystem; all its species, all their interactions and all their responses to stochastic influences. From such a model, it may be able to illustrate the repercussions of management strategies, so that management decisions can be tailored to the functioning of the ecosystem and therefore implement conservation relevant to the whole area. More importantly, it will hopefully provide a knowledge and understanding of this and other ecosystems on a level never before available.

2.3 MODELLING THE SERENGETI-MARA ECOSYSTEM

Without extensive amounts of data on all aspects of an ecosystem, the construction of a comprehensive model would be virtually impossible (Grainger 1999). The Serengeti-Mara ecosystem (as previous discussed in chapter 1) is, arguably, the only ecosystem for which there is such adequate data at present. Furthermore, research has focused on potential keystone species, or at least species that have a strong influence on the overall dynamics of the ecosystem (Watson 1966; Murray *et al.* 1992; Pascual *et al.* 1997; Hilborn & Mangel 1997; Mduma *et al.* 1998, 1999; Homewood *et al.* 2001). It is this abundance of data that provides a strong basis on which to construct a simulation that has the potential to encompass many elements of the ecosystem. Moreover, the occurrence of two major ecological perturbations within the last 40 years, the removal of rinderpest and a periodic increase in rainfall, provides the opportunity to test the model systematically.

The major objective of this thesis is to set-up a model with the potential to incorporate as many elements of the Serengeti-Mara ecosystem as possible, to give a fuller understanding of its functioning. The construction of such a complex model must focus initially on incorporating those components indicative of that ecosystem. Through this, the foundations are laid on which the remaining components can be integrated into the model. A component is defined as a species, or as a population within a species distinguished by its behaviour. For example, within the Serengeti there are two wildebeest components, one representing those wildebeest that migrate and the other that represents those that do not, generally referred to as resident (refer back to section 1.5.4).

As it is impossible to create a model for an entire ecosystem in the time it takes to do a PhD, its construction initially concentrated on building a foundation using those components considered to be dominant mediators. Designing the model in this way provides scope for its extension in the future. Therefore, the contents of this thesis can, in some ways, be considered a 'work in progress'. It tackles issues such as where to start modelling the ecosystem, what methods to use, what components to introduce, what data to use and how to test its accuracy. Furthermore, by working through these issues and developing the more influential portion of the model, an increased understanding of the basic dynamics within the ecosystem can be gained. Before commencing the model, its overall aims need to be defined, as in which components should be modelled at this stage and what benchmarks should they follow.

2.3.1 Components

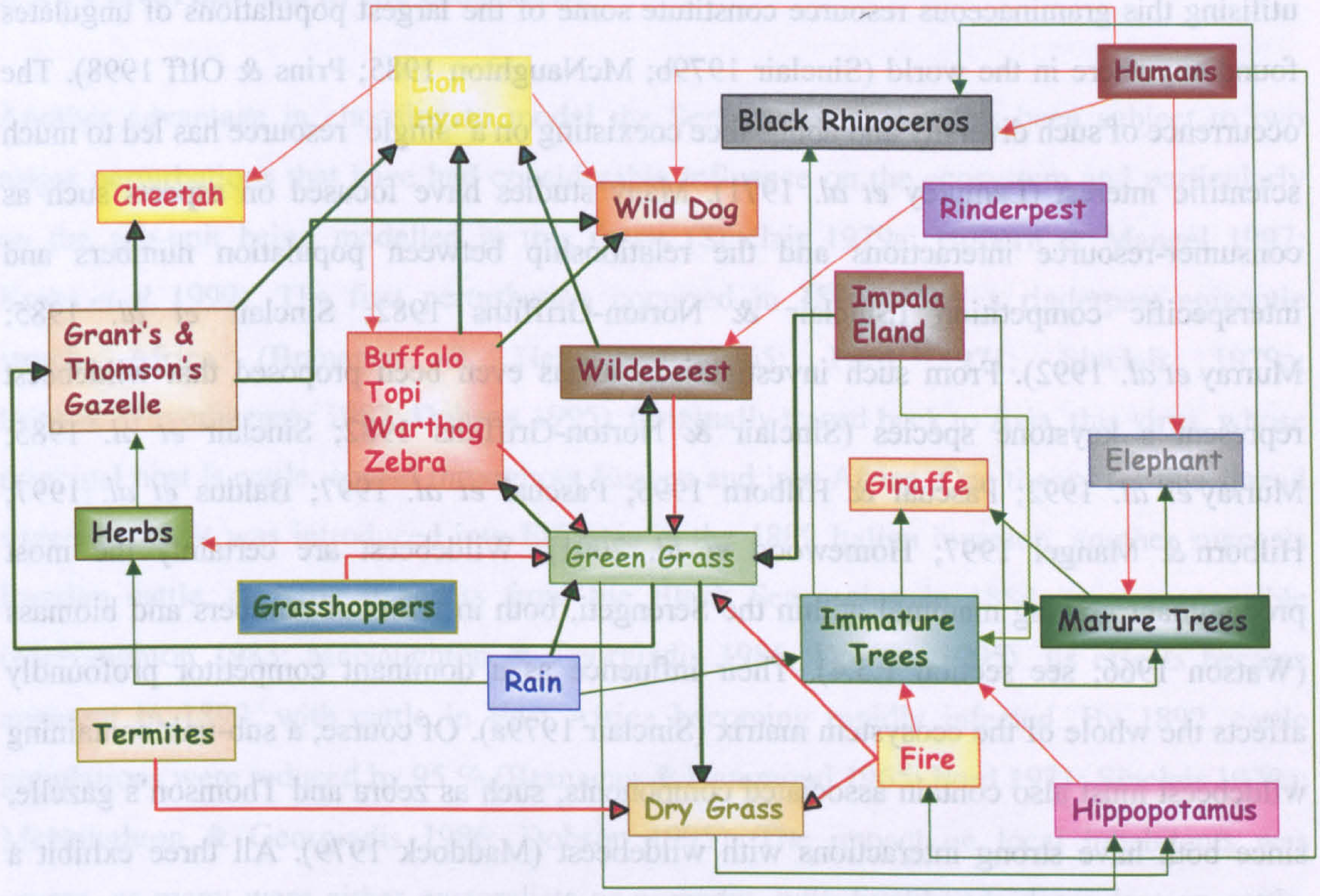

Figure 2.1 A flow diagram showing a selected number of the interactions between the components of the Serengeti-Mara ecosystem based on the literature. Red arrows indicate a negative interaction and green arrows indicate a positive interaction. Those arrows outlined in black indicate those interactions included in the initial construction of the model.

The Serengeti-Mara ecosystem is undeniably diverse, consisting of a large matrix of interacting components (Gichohi *et al.* 1996; Figure 2.1). For the purposes of this thesis, given the time-scale available, an isolated sub-unit of this matrix is considered in the initial construction of the model. The sub-unit selected is required to be relatively independent. That is, the dynamics of the components within that sub-unit should be maintained principally by their internal interactions (Walker & Noy-Meir 1982; Sinclair 1995b). In the Serengeti, it is evident that there are two such sub-units. In one, the major primary producer is grass and in the other, it is trees (McNaughton 1985; van de Koppel & Prins 1998;

Jefferies 1999). Both have a number of herbivores that are exclusively affiliated with them - grazers and browsers respectively. Of the mixed feeders exploiting both primary resources in the Serengeti, none are considered to be particularly influential in the dynamics of either sub-unit (Prins & Olff 1998). But which of the two sub-units is more crucial in the overall dynamics of the Serengeti ecosystem?

The answer is relatively simple. The Serengeti is primarily grassland and the herbivores utilising this graminaceous resource constitute some of the largest populations of ungulates found anywhere in the world (Sinclair 1979b; McNaughton 1985; Prins & Olff 1998). The occurrence of such diversity and abundance coexisting on a 'single' resource has led to much scientific interest (Lamprey *et al.* 1971). Many studies have focused on aspects such as consumer-resource interactions and the relationship between population numbers and interspecific competition (Sinclair & Norton-Griffiths 1982; Sinclair *et al.* 1985; Murray *et al.* 1992). From such investigations it has even been proposed that wildebeest represent a keystone species (Sinclair & Norton-Griffiths 1982; Sinclair *et al.* 1985; Murray *et al.* 1992; Pascual & Hilborn 1995; Pascual *et al.* 1997; Baldus *et al.* 1997; Hilborn & Mangel 1997; Homewood *et al.* 2001). Wildebeest are certainly the most predominant grazing mammal within the Serengeti, both in terms of numbers and biomass (Watson 1966; see section 1.5.4). Their influence as a dominant competitor profoundly affects the whole of the ecosystem matrix (Sinclair 1979a). Of course, a sub-unit containing wildebeest must also contain associated components, such as zebra and Thomson's gazelle, since both have strong interactions with wildebeest (Maddock 1979). All three exhibit a similar migratory behaviour, exploiting grass in the same general area at approximately the same time. Furthermore, the large-scale movements of these components off the plains in the dry season influences the intensity of competition not only for these migrants, but also for those resident herds found throughout the Serengeti (Sinclair 1979a). To incorporate these spatial and temporal dependent interactions into the model, and thus take a more realistic approach, resident components need to be included, such as buffalo, impala, Coke's hartebeest, Thomson's gazelle, wildebeest, zebra, Grant's gazelle and topi.

The predation of all these herbivore components is also an important factor in reconstructing the Serengeti ecosystem. Five large predator species have been identified in the Serengeti; lion, leopard, cheetah, spotted hyaena and African wild dog (Hofer *et al.* 1993; Nowell & Jackson 1996; Woodroffe *et al.* 1997; Mills & Hofer 1998). The latter are of particular interest because they are highly endangered within Africa and over the last 40 years have decreased in numbers considerably, so much so that they are now extinct in the Serengeti (Frame *et al.* 1979; Burrows *et al.* 1994; Ginsberg *et al.* 1995; Woodroffe *et al.* 1997).

Although, individual predator dynamics are not being considered specifically at this stage in the model, its continued construction may further increase our understanding of the wild dog's demise. Primarily, this thesis aims to discover the degree of influence each of these predators has on the dynamics and structure of the grazing herbivore populations, by determining their differential use of potential prey, habitat use and hunting methods (Gichohi *et al.* 1996; Meffe *et al.* 1997).

2.3.2 Perturbations to the ecosystem

Another advantage in choosing to model the Serengeti is that it has been subject to two major perturbations that have had considerable influence on the ecosystem and particularly on the sub-unit being modelled in this thesis (Sinclair 1979a; Hilborn & Mangel 1997; Krebs *et al.* 1999). The first perturbation occurred in 1890, when a rinderpest epizootic struck Africa (Branagan & Hammond 1965; Ford 1971; Sinclair 1979a; Prins & Weyerhaeuser 1987; Dobson 1995). Originally traced back to Asia, this virus, whose principal host is cattle, spread throughout Europe and into Africa. One theory for this spread suggests that it was introduced into Ethiopia in the 1889 Italian invasion, another suggests Russian cattle, carrying it across from the Black Sea region in 1884, were responsible (McNaughton 1983; McNaughton & Georgiadis 1986; Dobson 1995). Its effects became apparent in 1890, with cattle in East Africa becoming rapidly infected. By 1892, cattle populations were reduced by 95 % (Branagan & Hammond 1965; Ford 1971; Sinclair 1979a; McNaughton & Georgiadis 1986; Dobson 1995). The impact on local inhabitants was severe, as many were either pastoralists or nomadic, with livelihoods dependent on cattle. However, the domestic populations were not the only ones to suffer, as rinderpest decimated the wild Artiodactyla populations, particularly those closely related to cattle, such as buffalo and wildebeest (Sinclair 1977b; Plowright 1982; Prins & Weyerhaeuser 1987; Dobson 1995; Krebs *et al.* 1999). In 1933, it was observed that rinderpest mortality became an annual event at the end of the dry season. It was soon realised this coincided with the weaning of young when they no longer received immunity from their mothers and subsequently contracted the disease (Talbot & Talbot 1963; Branagan & Hammond 1965; Ford 1971; Sinclair 1973b, 1979a; McNaughton & Georgiadis 1986). Those few that survived were fortunate to have developed their own immunity (Talbot & Talbot 1963). In 1952 the general immunisation of cattle was introduced. This vaccination scheme was fully implemented by 1960 and by 1963 rinderpest was completely eradicated from cattle and wild ungulates in the Serengeti area (Plowright 1982; Alexander 1986; Dobson 1995).

Consequently, the removal of this limiting factor influenced the population dynamics of not only two major herbivores, but of many other components through a cascading effect. This was initially evident in the immediate, near 100 %, increase in wildebeest yearling survival. This in turn, led to a considerable increase in the total population size by 1967 (Branagan & Hammond 1965; Ford 1971; Sinclair 1979a; Plowright 1982; McNaughton 1983; Krebs *et al.* 1999). A similar increase was monitored in the buffalo population (Sinclair 1973b; Plowright 1982; McNaughton 1983).

The second perturbation occurred a decade later, brought about by a change in rainfall patterns. Between 1971 and 1976, rainfall became consistently higher than previously recorded, with the average dry season rainfall increasing from 150 mm to 250 mm (Sinclair 1979a, Krebs *et al.* 1999; Wolanski *et al.* 1999). As a result, the level of grass growth intensified and led to yet further, very noticeable population increases in both wildebeest and buffalo (Sinclair 1979c; Sinclair & Norton-Griffiths 1982, Sinclair *et al.* 1985, Rodgers & Swai 1988). By 1977, for instance, wildebeest numbers were recorded to have risen from 500,000 animals a decade earlier, to 1.3 million (Sinclair 1979a; Rodgers & Swai 1988). It is these events that have enhanced the dynamics of the Serengeti-Mara ecosystem, providing a rare opportunity to assess the types and strengths of interactions occurring between its components (Sinclair 1979a; Krebs *et al.* 1999). Moreover, these perturbations can be used to determine whether the extent of each interaction is represented appropriately in the model as it should simulate historical trends in the face of these two events. With these objectives in mind, the final step is to propose software capable of simulating such a model.

2.3.3 Computer Software

Currently, there are many biology-related modelling packages available, perhaps a further indication of the increasing popularity of this technique (see www.wiz.uni-kassel.de/ecobas.html; Walker & Crout 1997). For instance, Boone *et al.* (2002) use a series of interconnecting Fortran programs in their SAVANNAH model for the Ngorongoro Conservation Area, while Gignoux *et al.* (1998) use MUSE, the Multistrata Spatially Explicit computer program. However, a large proportion of these software programs have been designed for a specific purpose and allows only simple parameters and starting values to be varied. Any more substantial changes to the program require modifications to the software. This in itself may prove difficult without an in depth knowledge of the programming involved.

The focus of this thesis is to simulate a sub-unit of the Serengeti-Mara ecosystem designed on the basis that with continued work the whole ecosystem could be included. Central to the choice of software is the prospect that the complete model could potentially be distributed publicly as a tool to develop management strategies for the future conservation of the Serengeti and even other similar African ecosystems. By creating the model in software that is user–friendly and readily accessible to all, these future goals may be accomplished. It is considered that a software application that provides these criteria is Microsoft Excel, as it is readily available, easy to use, versatile and capable of dealing with such a complex model. Intriguingly, spreadsheets such as Excel and Lotus 123 have also been recently proposed by other modellers as suitable modelling and simulation tools (Hilborn & Mangel 1997; Manly 1997).

2.4 GENERAL SCOPE OF THESIS

The layout of this thesis follows the process involved in constructing the model, with each chapter representing a stage in its construction. In chapter 3, the spatial and temporal heterogeneity that occurs within the Serengeti-Mara ecosystem is discussed. It outlines how relatively large-scale variations can have a considerable impact on the overall dynamics of the ecosystem and thus makes it inappropriate for it to be treated uniformly. Consequently, six modules are defined based on the area's spatial and temporal variations, such as rainfall, humidity, habitat structure and species presence (Figure 2.2). Dynamics specific to each module can then be used to gain a more accurate representation of the overall abundance of different populations within the ecosystem.

Figure 2.2 Six modules defined by spatial and temporal characteristics that occur within the Serengeti-Mara ecosystem.

The following chapter then initiates the model by introducing the most basic of variables, rainfall. Using the appropriate annual rainfall measurements for each module and the defined relationship between grass growth and rainfall, as found in the literature, the amount of grass produced is calculated. However, chapter 4 also takes into account that the amount of grass produced does not simple represent the amount of grass that is available to large grazing herbivores. Consequently, factors that influence grass availability are included into the modules, such as fire, grass maturation and insect and small mammal herbivory. Based on annual grass availability, chapter 5 focuses on determining the survival of the migratory wildebeest. This also incorporates relative metabolic rates as indicators of food requirements, life history parameters to ascertain the varying survival of separate age groups and reproductive strategies specific to the migratory wildebeest to estimate their annual recruitment. Chapter 6 then outlines the specific modifications required in order to apply this method to migratory Thomson's gazelle and zebra, and other resident components included in the model at this stage. The chapter also incorporates interspecific competition between all these grazing herbivore components. As the total weekly amount of grass available is dependent upon the amount of grass consumed in the previous week, the total consumption of grass by the large herbivores within each module is used to determine the amount of uneaten grass available to them the following week. The average weekly amount of grass available for a specific module is then used to estimate the survival of individuals within it. As the survival of large herbivores is also affected by predation, this factor is included in the model and discussed in chapter 7. Within this chapter, the number and type of large herbivores that fall prey to each of the five large carnivores is estimated. These figures are based on carnivore population numbers, minimum food requirements calculated again from relative metabolic rates and prey preferences as taken from the literature. Following the inclusion of predation, the model is run (see summary flow chart given in figure 2.3) and its accuracy in representing the Serengeti-Mara ecosystem is examined (Chapter 8). Potential explanations for divergence away from actual population numbers are proposed and appropriate alterations are made and compared. Subsequently, the model is discussed in terms of its success, not only as a working model, but in providing information on the processes and mechanisms that influence and regulate its components (Chapter 9). Finally, its effectiveness as a conservation tool, how it can be implemented even in these early stages, and what direction future work on this model should take are considered. A CD containing the Serengeti-Mara ecosystem model, associated work and a user guide can be found at the back of this thesis.

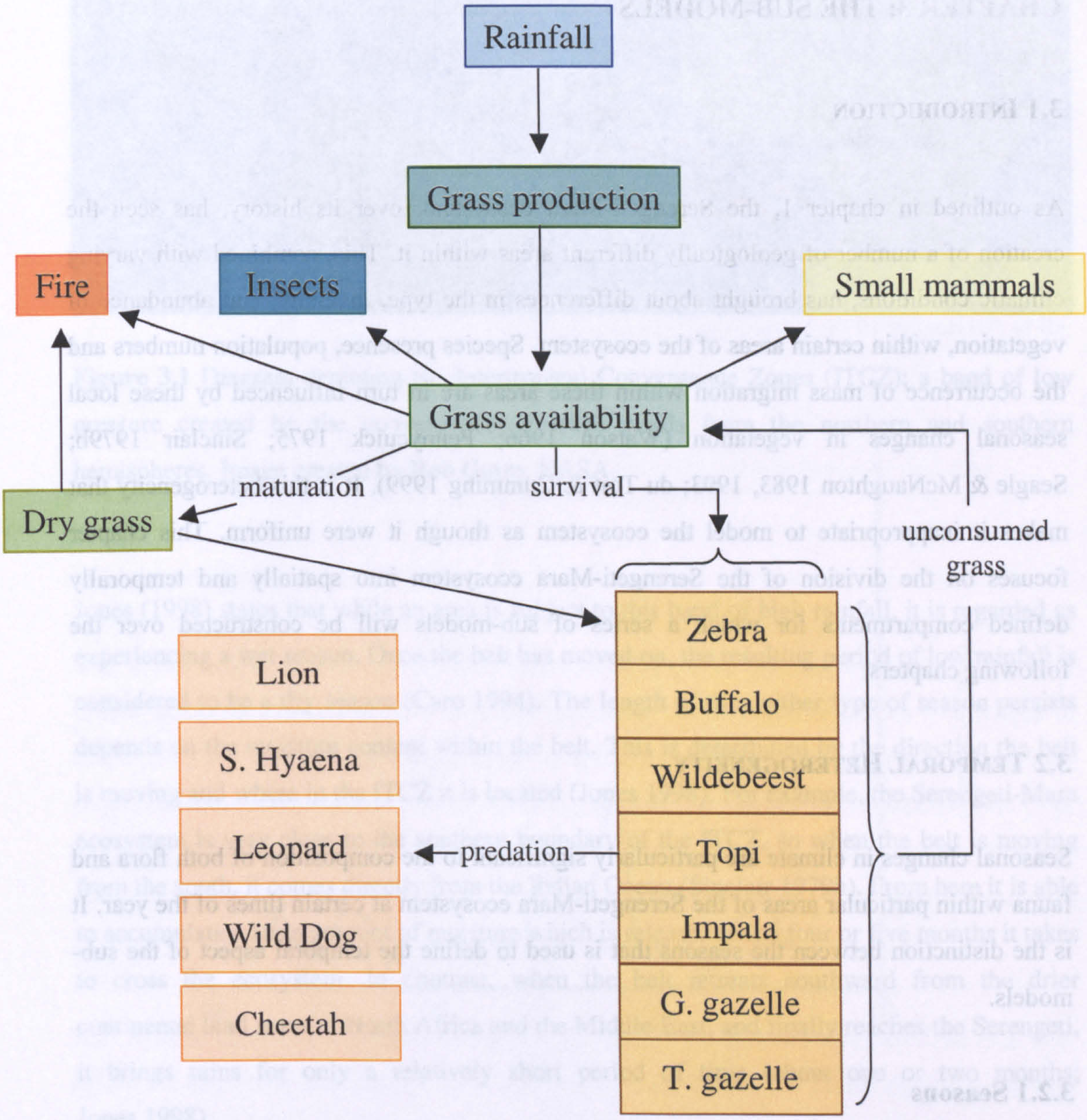

Figure 2.3 Flow diagram showing the components of the Serengeti-Mara ecosystem and the factors that may have an influence on their dynamics included in the initial construction of the model.

CHAPTER 3: THE SUB-MODELS

3.1 INTRODUCTION

As outlined in chapter 1, the Serengeti-Mara ecosystem, over its history, has seen the creation of a number of geologically different areas within it. This, combined with varying climatic conditions, has brought about differences in the type, diversity, and abundance of vegetation, within certain areas of the ecosystem. Species presence, population numbers and the occurrence of mass migration within these areas are in turn influenced by these local seasonal changes in vegetation (Watson 1966; Pennycuick 1975; Sinclair 1979b; Seagle & McNaughton 1983, 1993; du Toit & Cumming 1999). It is this heterogeneity that makes it inappropriate to model the ecosystem as though it were uniform. This chapter focuses on the division of the Serengeti-Mara ecosystem into spatially and temporally defined compartments for which a series of sub-models will be constructed over the following chapters.

3.2 TEMPORAL HETEROGENEITY

Seasonal changes in climate are particularly significant to the composition of both flora and fauna within particular areas of the Serengeti-Mara ecosystem at certain times of the year. It is the distinction between the seasons that is used to define the temporal aspect of the sub-models.

3.2.1 Seasons

In the Serengeti two seasons can be easily recognised. Their division is based on the fluctuation of rainfall between certain times of the year. This variation in rainfall is the result of the ecosystem lying within the Intertropical Convergence Zone (ITCZ), an area that circles the Earth near the equator (Norton-Griffiths *et al.* 1975; McNaughton 1985; Gichohi *et al.* 1996; Jones 1998; Figure 3.1). Within this zone exists a latitudinal belt of low pressure, marking the convergence of dry, hot air to the north and warm humid air to the south. Here, a band of hot air is formed, constantly accumulating moisture, which rises, cools and is released in an almost perpetual series of thunderstorms (Pearsall 1957; Jones 1998). This belt moves back and forth across the equator within the ITCZ, following six weeks behind the sun (Gichohi *et al.* 1996). It reaches its most northerly position in late July and most southerly position in late January (Norton-Griffiths *et al.* 1975; Jones 1998).

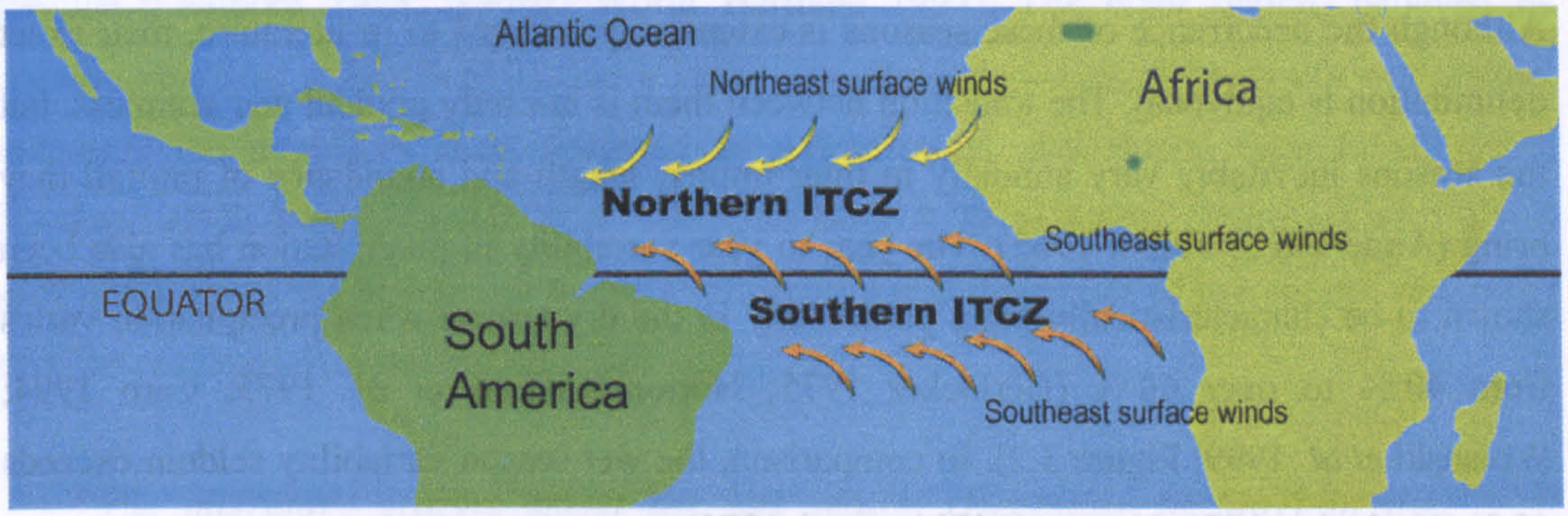

Figure 3.1 Diagram depicting the Intertropical Convergence Zones (ITCZ); a band of low pressure created by the convergence of trade winds from the northern and southern hemispheres. Image created by Rob Gutro, NASA.

Jones (1998) states that while an area is subject to this band of high rainfall, it is regarded as experiencing a wet season. Once the belt has moved on, the resulting period of low rainfall is considered to be a dry season (Caro 1994). The length of time either type of season persists depends on the moisture content within the belt. This is determined by the direction the belt is moving and where in the ITCZ it is located (Jones 1998). For example, the Serengeti-Mara ecosystem is very close to the southern boundary of the ITCZ, so when the belt is moving from the south, it comes directly from the Indian Ocean (Sinclair 1979b). From here it is able to accumulate a large amount of moisture which is released in the four or five months it takes to cross the ecosystem. In contrast, when the belt retreats southward from the drier continental land mass of North Africa and the Middle-East, and finally reaches the Serengeti, it brings rains for only a relatively short period of time (about one or two months; Jones 1998).

The length of the dry season that occurs after the belt has passed is also dependent on an area's location within the ITCZ (Jones 1998). For example, in Nairobi, a short dry season follows the short wet season and corresponds to the time it takes for the southward-moving belt to reach the edge of the ITCZ and return (Caro 1994; Hillman & Hillman 1997). As the Serengeti-Mara ecosystem is even closer to the edge of the ITCZ than Nairobi, the end of the short wet season is almost immediately followed by the start of the long wet season, making the short dry season indistinct (Herlocker 1975; Sinclair 1979b; Caro 1994; Jones 1998). It therefore appears that the ecosystem has one long wet season and one fairly long dry season, annually.

Although the occurrence of these seasons is extensively referred to in literature, their exact delimitation is equivocal. The transition between them is not only gradual and seamless, but the seasons inevitably vary annually in their timing, length and abundance of rainfall they bring (Anderson & Talbot 1965). The year to year variability in precipitation has also been shown to be characteristically high, particularly in the dry season when precipitation varies from 40 % to over 60 % (Herlocker 1975; Norton-Griffiths *et al.* 1975; Caro 1994; Wolanski *et al.* 1999; Figure 3.2). In comparison, the wet season variability seldom exceeds 40 % (Herlocker 1975; Norton-Griffiths *et al.* 1975).

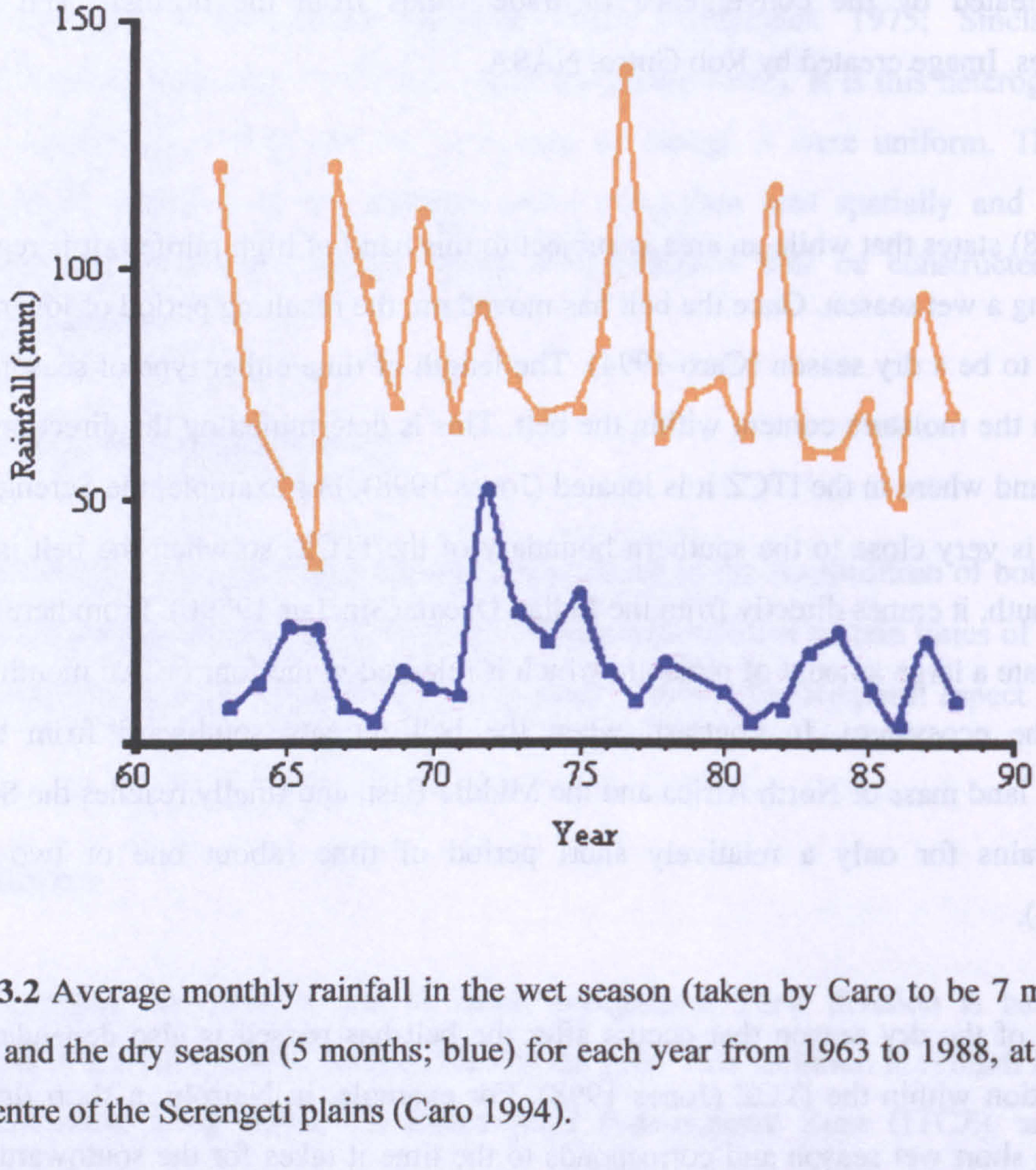

Figure 3.2 Average monthly rainfall in the wet season (taken by Caro to be 7 months long; orange) and the dry season (5 months; blue) for each year from 1963 to 1988, at Naabi Hills in the centre of the Serengeti plains (Caro 1994).

This has caused controversy between different researchers in defining the wet and dry season. For the model, the majority opinion was adopted, dividing the year into a seven-month wet season, starting in November, and a five-month dry season, starting in June (Talbot & Talbot 1963; Estes 1966; Bell 1969; Kruuk 1972; Schaller 1972; Braun 1973; Croze 1974a; IUCN 1974; Herlocker 1975;. Kreulen 1975; Norton-Griffiths *et al.* 1975; McNaughton 1985; Fryxell *et al.* 1988; Caro 1994; Mduma & Sinclair 1994;

Pascual & Hilborn 1995; Natural World Heritage 1997). The other option, believed by considerably less researchers, is that a year to be divided into an eight month wet season, including the month of June, followed by a four-month dry season (von Frisch 1969; Sinclair 1974d, 1985; Sinclair *et al.* 1985; de Boer & Prins 1990). There are also a few publications that say something entirely different, a possible result of the annual variability that has occurred over the last 40 years.

> "*The migratory grazers spend the wet season (December to May) in the Serengeti plains, migrate to the western corridor at the end of the wet season and then migrate to the northern extension and into Kenya for the dry season grazing*" (Belsky 1985).
>
> "*Rainfall is strongly seasonal - 'short rains' about December being followed by a main rainy season in April –June.*" (Pearsall 1957)

An example of monthly rainfall, given by Schmidt (1975), for an area within the north west of the Serengeti, particularly reinforces the seven to five month seasonal division, with a clear distinction seen between the two seasons (Figure 3.3). Furthermore, a description of rainfall given by Norton-Griffiths *et al.* (1975) portrays a very similar pattern to that seen in figure 3.3. They identify two rainfall peaks in the wet season, the only clear identification of a separate short and long wet season. From the start of the rains in November the first peak occurs in December. From January through to March, monthly rainfall is lower and is followed by the second peak in April, the wettest month of the year. During the dry season monthly rainfall is much lower, with July being the driest month.

The occurrence of two distinct seasons is predominant across the ecosystem. For example, figure 3.4 illustrates this pattern in data given by Caro (1994) for Naabi on the south-east plains and figure 3.5 represents the mean rainfall at Banagi Station, located within the centre of the Serengeti-Mara. Here, a separation of over 30 mm of rainfall differentiates the two seasons (Anderson & Talbot 1965). Such examples inspire further confidence in the use of a seven-month wet season and five-month dry season to represent the temporal aspect of the sub-models.

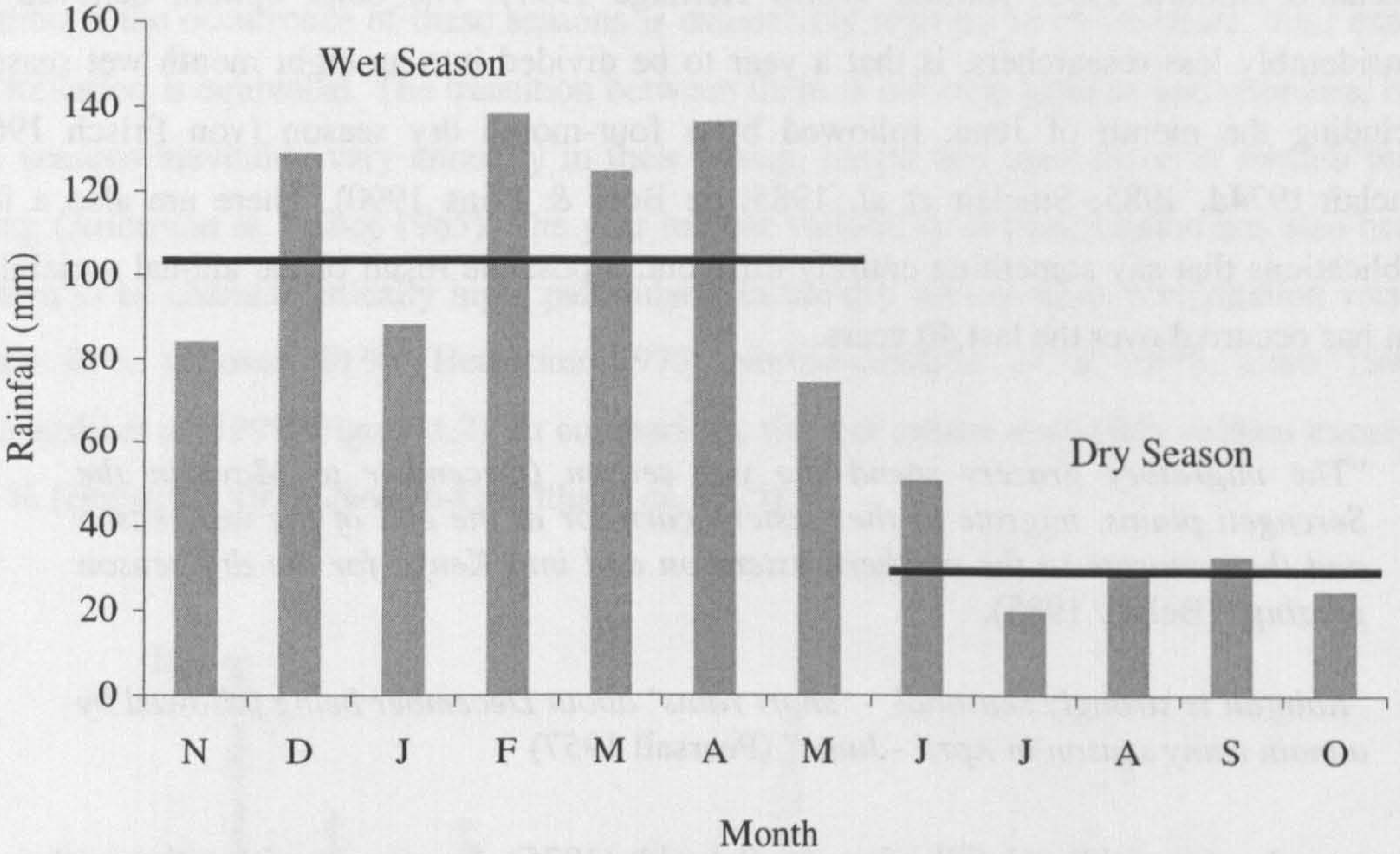

Figure 3.3 Seasonal pattern in monthly rainfall in the north west of the Serengeti-Mara ecosystem (Schmidt 1975). Two different stations, Klein's Camp and Bologonia are used. Black lines indicate seasonal averages.

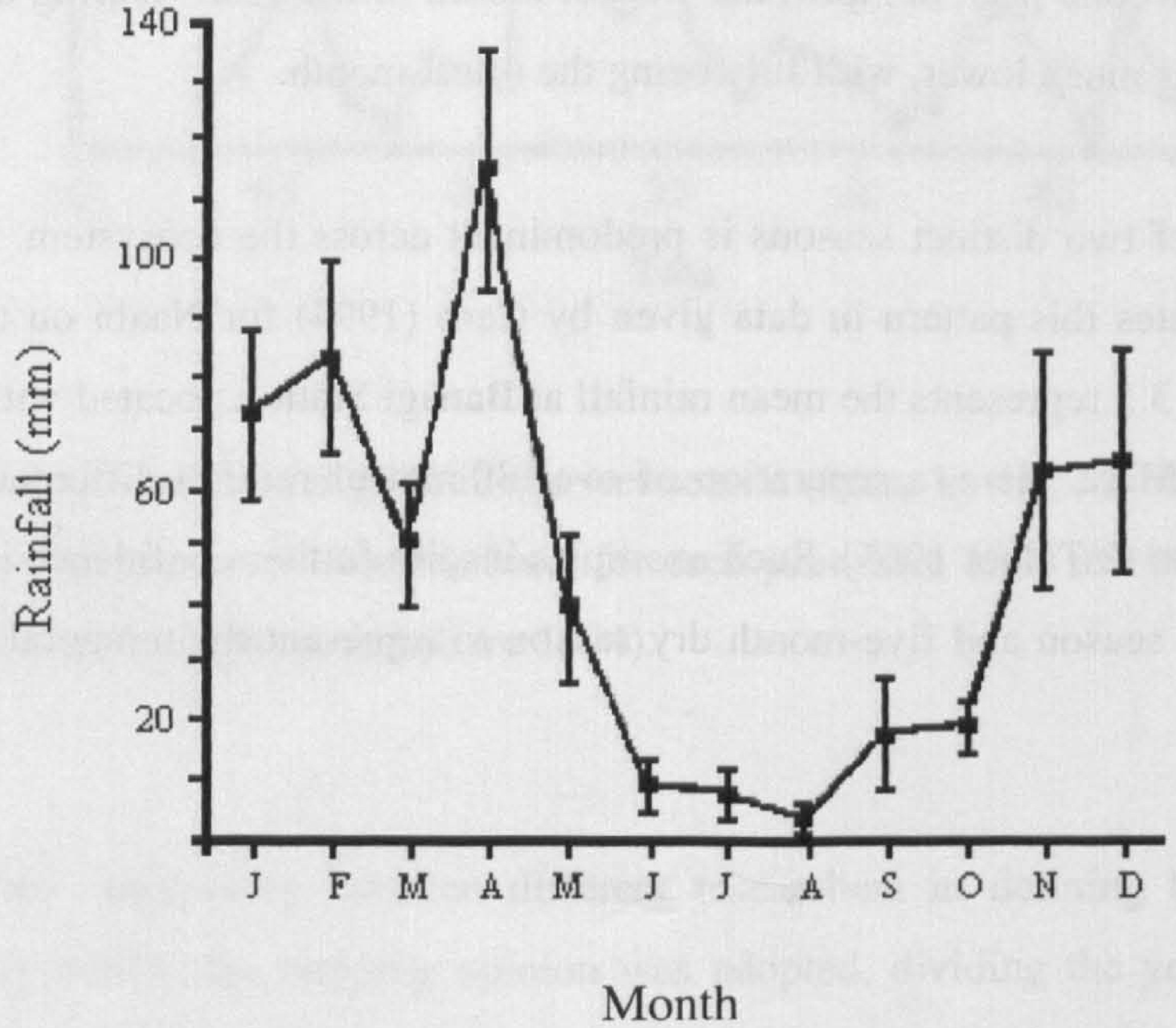

Figure 3.4 Average (and SE) monthly rainfall at Naabi North rain gauge, in the centre of the Serengeti plains, between 1980 and 1988 (Caro 1994).

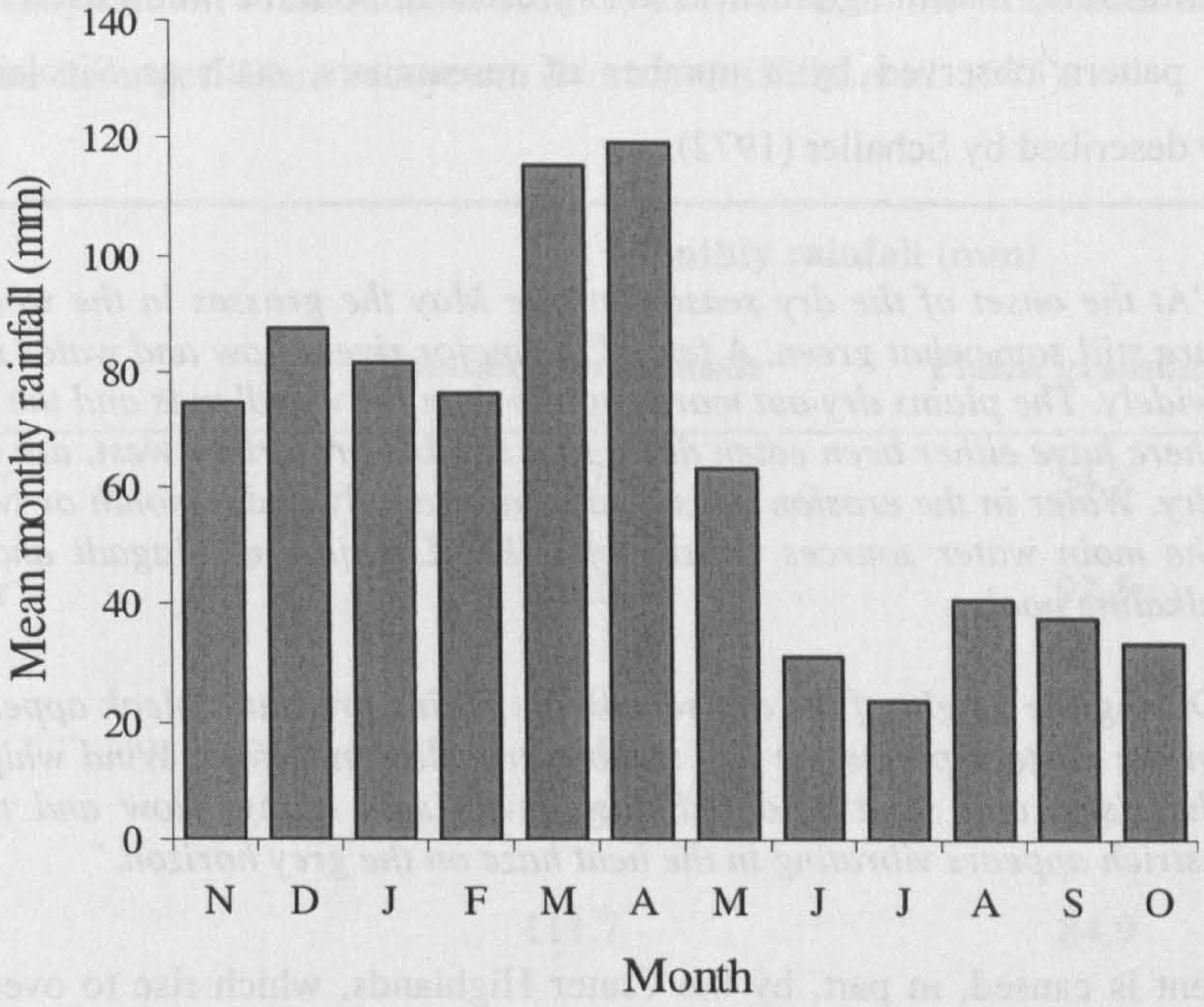

Figure 3.5 Mean monthly rainfall recorded over 24 years in Banagi Station situated in the centre of the Serengeti-Mara ecosystem (Anderson & Talbot 1965).

3.3 SPATIAL HETEROGENEITY

In addition to the temporal variation mentioned in the last section, the Serengeti ecosystem also varies spatially (Chapter 1). To accommodate this spatial variation into the model, the Serengeti region was divided into specific zones according to related aspects, such as rainfall, humidity, habitat structure and large herbivore migration.

3.3.1 Rainfall Gradients

The first aspect used to define spatially distinct areas within the ecosystem is rainfall. Local topography within the Serengeti area has created a rainfall gradient. This gradient produces clear differences in the intensity of rainfall that occurs between the southern and northern parts of the ecosystem, with the northern region receiving a greater proportion of the rainfall (Table 3.1 Braun 1973; Norton-Griffiths *et al.* 1975; McNaughton 1979a, 1985; Seagle & McNaughton 1993; Mduma *et al.* 1999; Wolanski *et al.* 1999).

Table 3.1 illustrates that the gradient is also present in both the wet season and dry season. This is a pattern observed by a number of researchers, such as Sinclair (1979b) and eloquently described by Schaller (1972).

> *"At the onset of the dry season in late May the grasses in the woodlands are still somewhat green. A few of the major rivers flow and water is found widely. The plains dry out more rapidly than the woodlands and the grasses there have either been eaten down to a stubble or, farther west, are tall and dry. Water in the erosion pans disappears rapidly and a month or two later the main water sources consist of Lakes Lagaja and Magadi and a few alkaline pools.*
>
> *During the height of the dry season the plains present a bleak appearance. In the eastern plains the dry stubble crackles underfoot. Wind whips over the rises, and sand coloured dust devils spin along. Now and then an ostrich appears vibrating in the heat haze on the grey horizon."*

This gradient is caused, in part, by the Crater Highlands, which rise to over 3,000 m and form a rain shadow preventing a considerable proportion of the rain from reaching the south-east plains (Norton-Griffiths *et al.* 1975). A gradient of increasing rainfall is generated from here and stretches across the ecosystem to the north-west woodlands on the Mara River (Table 3.2). The direction and intensity of this rainfall gradient during a wet season in the Serengeti region is shown in Figure 3.6 (Sinclair 1979b).

During the dry season the gradient is more pronounced and is associated with the wetter Congo weather system coming in from the west and increased humidity around Lake Victoria (Norton-Griffiths *et al.* 1975; McNaughton 1985). Both significantly contribute to increased precipitation in the northern extension and the western corridor during the dry season (Sinclair 1975, 1979b). Figure 3.7 shows the varying monthly rainfall distributions at several stations in the ecosystem. It illustrates the extent to which the combined effect of local features, such as increased humidity to the north and the rain shadow created by the Crater Highlands to the south, influence annual rainfall abundance across the ecosystem.

Table 3.1 Monthly rainfall in millimetres from 1962 to 1972, in the woodlands and southern grasslands of the Serengeti-Mara ecosystem (Norton-Griffiths *et al.* 1975).

	Monthly rainfall (mm)	
Month	**Northern woodlands**	**Plains grasslands**
November	98.7	54.7
December	101.8	92.5
January	87.0	77.7
February	82.5	87.4
March	111.7	84.9
April	150.2	88.1
May	92.3	47.4
Wet season total (mm)	**768.5**	**558.9**
June	44.3	26.2
July	15.9	5.2
August	31.2	11.5
September	38.3	17.2
October	46.4	20.4
Dry season total (mm)	**131.8**	**54.3**

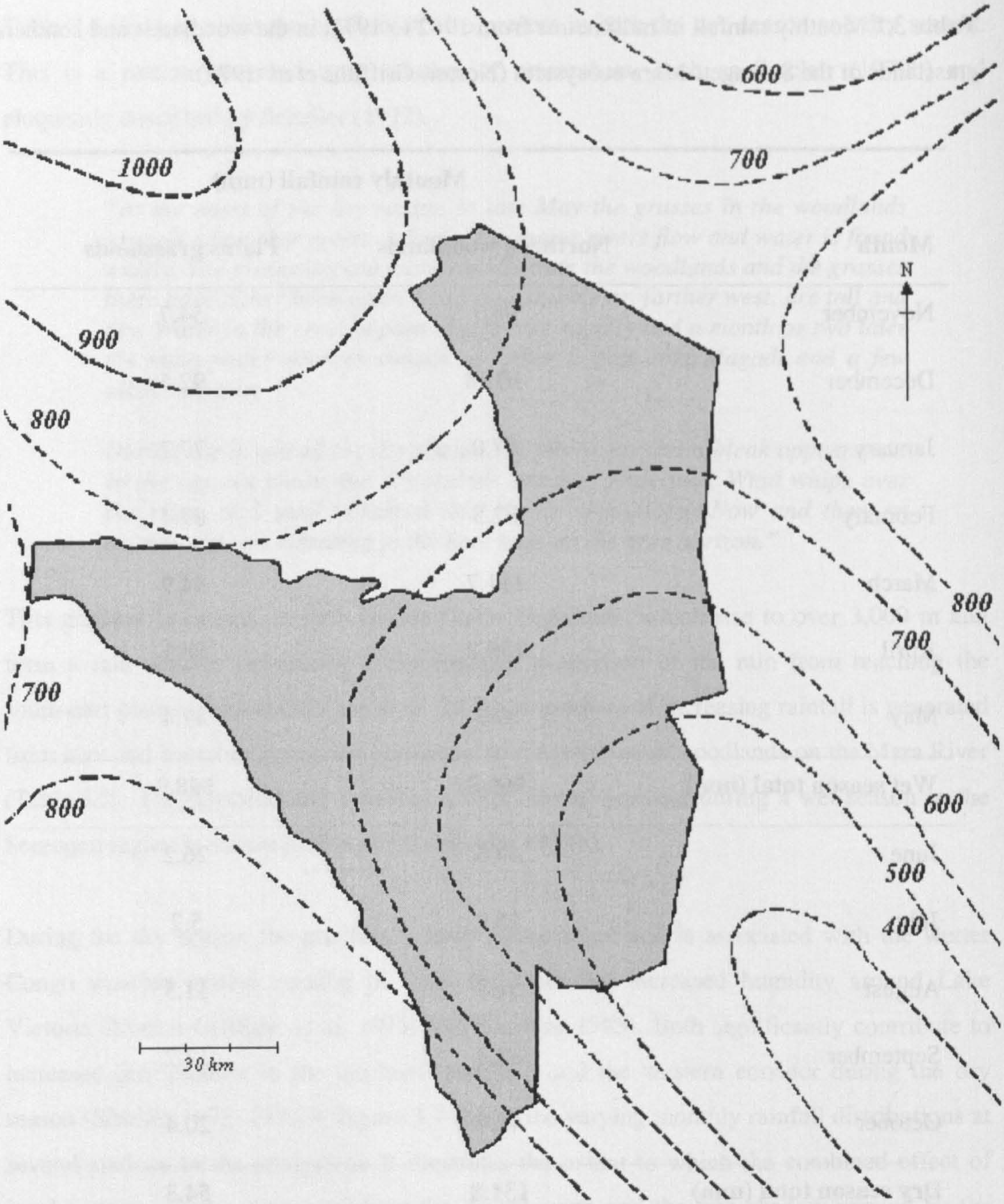

Figure 3.6 Mean wet-season rainfall isohyets (broken lines, mm) show a gradient of high rainfall in the north-west decreasing towards the south-west of the Serengeti National Park, shown in grey (Norton-Griffiths 1975; Sinclair 1979b).

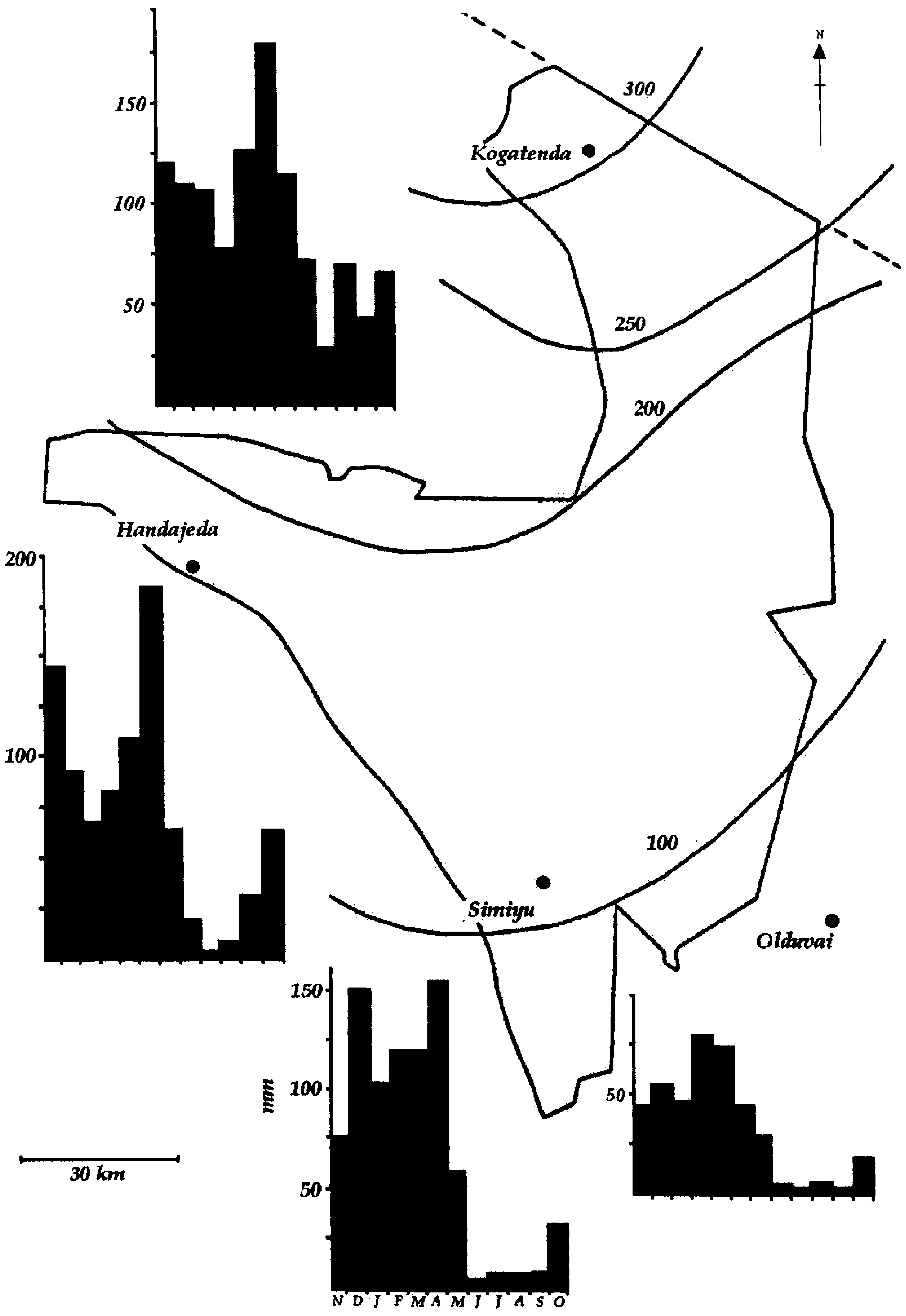

Figure 3.7 Mean dry season rainfall isohyets (mm) showing a gradient from high in the north west, to low in the south east, with histograms illustrating the distribution of rainfall throughout the year at the four stations indicated on the map (Sinclair 1977b).

Pennycuick (1975) also showed that a spatial pattern in the annual rainfall between 1960 and 1973 emerged in the form of three zones (Table 3.2). The first zone encompasses the plains, as this area receives the least amount of rain each year. A second zone of significantly increased rainfall lies within the central region of the Serengeti, consisting of a portion of the lower half of the northern extension and eastern half of the western corridor. The third zone incorporates both the remaining western corridor and northern extension and is typified by its higher rainfall abundance. Furthermore, Sinclair (1979b) suggests that the difference between these areas is consistent from year to year.

Table 3.2 Rainfall for each land region given in Pennycuick (1975). The three rainfall areas are indicated by shading.

Region	Rainfall (mm)		
	Annual	Wet Season	Dry season
North	1117	862	255
	1057	806	251
	1083	836	247
	1046	802	244
West	927	751	176
	1042	867	175
	992	820	172
	1003	844	159
Central	806	641	165
	709	662	128
Plains	590	511	79
	710	619	91
	842	743	99

3.3.2 Humidity

Humidity levels within the ecosystem further reflect the rainfall gradient. Norton-Griffiths *et al.* (1975) constructed what they call a climatogram showing monthly rainfall and the corresponding humidity levels for five regions of the Serengeti. The regions include the upper and lower half of the northern extension, the east and west side of the western corridor, and the plains (Figure 3.8). These show that humidity on the plains is considerably lower than all other regions. Figure 3.8 also shows that the lower portion of the northern extension and the eastern half of the western corridor appear to be fairly similar in their humidity levels, as are the upper portion and western half.

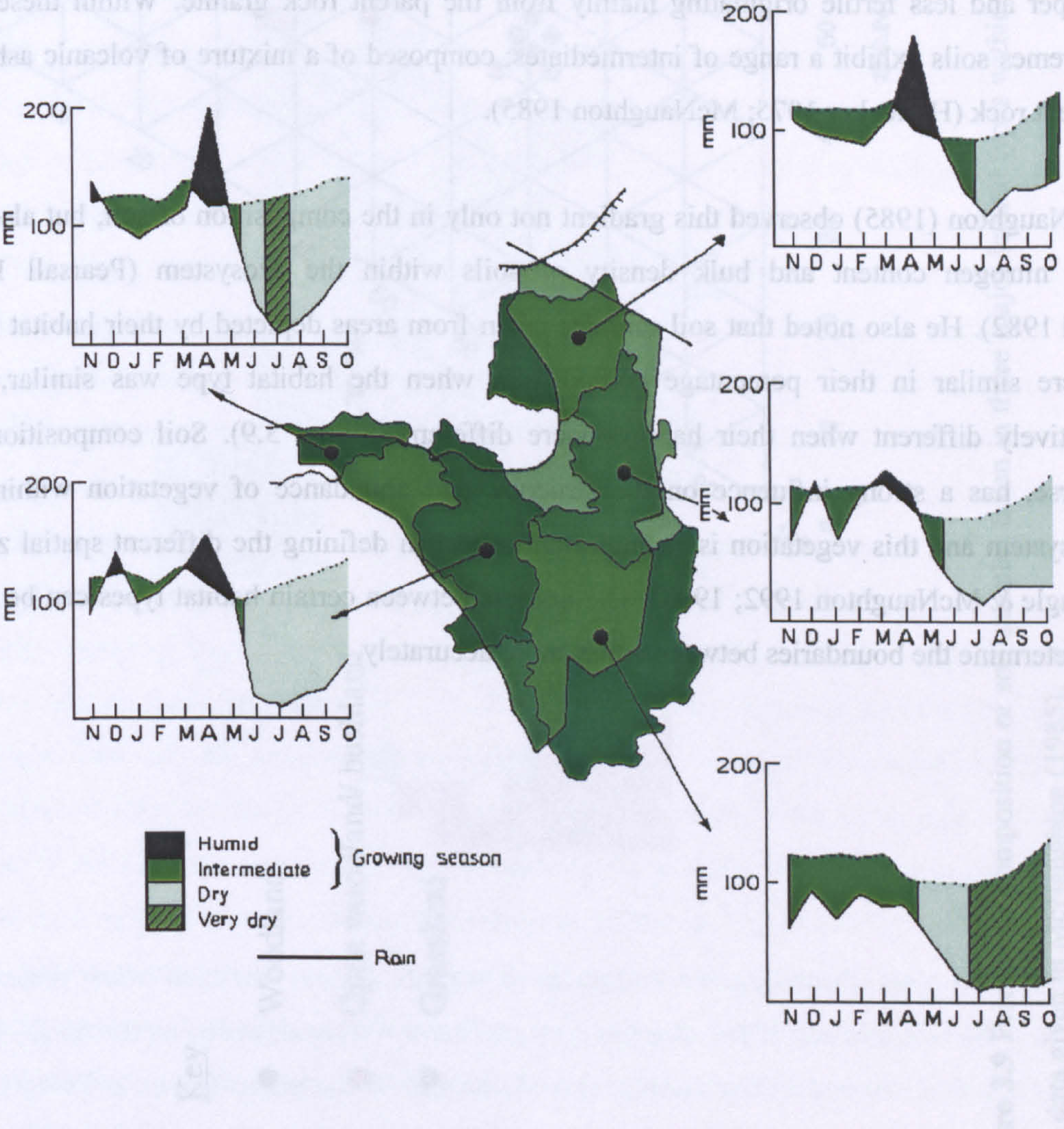

Figure 3.8 Climatograms for five selected land regions within the Serengeti-Mara ecosystem, illustrating monthly humidity (coloured areas and dashed black line) and rainfall (solid black line) (Norton-Griffiths *et al.* 1975).

By combining the areas that are similar in terms of humidity, three separate zones are again identified within the ecosystem. These zones can be used to represent the spatial aspect of the sub-models, although their borders are not that clearly defined.

3.3.3 Soil gradient

As discussed in section 1.4.2, soil composition varies across the ecosystem due to a history of volcanic activity. This has led to the creation of a soil gradient, coincidentally similar to the rainfall gradient. It stretches across the ecosystem from the south-east, where ash deposited by volcanic activity in the Crater Highlands has resulted in the formation of shallow, fertile, sandy soils with an underlying calcium carbonate hardpan (Seagle & McNaughton 1992, 1993). At the other extreme, in the north-west, soils are deeper and less fertile originating mainly from the parent rock granite. Within these two extremes soils exhibit a range of intermediates, composed of a mixture of volcanic ash and parent rock (Herlocker 1975; McNaughton 1985).

McNaughton (1985) observed this gradient not only in the composition of soil, but also the pH, nitrogen content and bulk density of soils within the ecosystem (Pearsall 1957; Bell 1982). He also noted that soil samples taken from areas depicted by their habitat type, where similar in their percentage composition when the habitat type was similar, and relatively different when their habitats were different (Figure 3.9). Soil composition, of course, has a strong influence on the structure and abundance of vegetation within the ecosystem and this vegetation is an important aspect in defining the different spatial zones (Seagle & McNaughton 1992; 1993). The borders between certain habitat types can be used to determine the boundaries between zones more accurately.

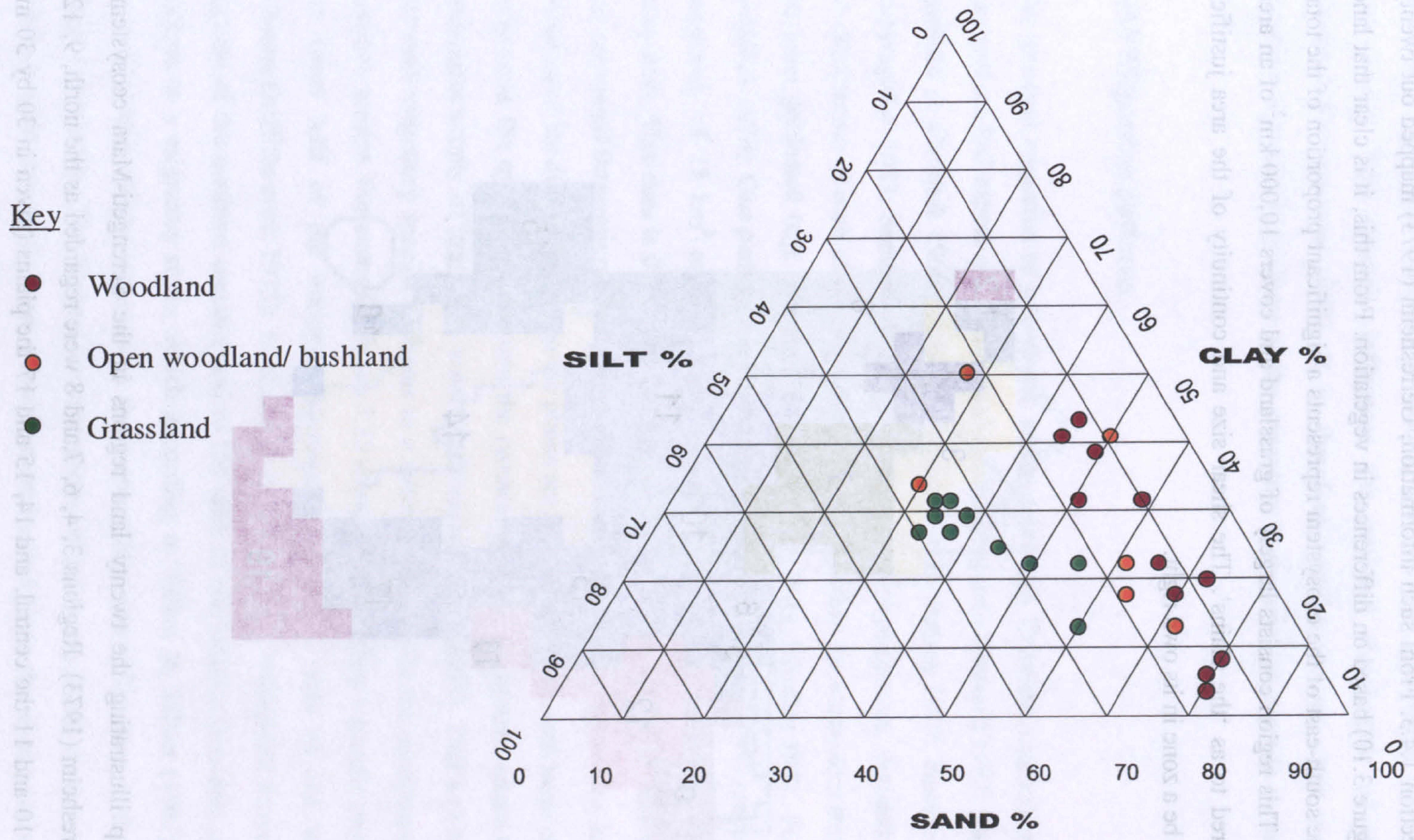

Figure 3.9 Percentage composition of soil samples taken in three major habitat types within the Serengeti Mara ecosystem, illustrated from data given in McNaughton (1985).

3.3.4 Distribution of Vegetation

Details of the distribution and types of vegetation within the Serengeti-Mara ecosystem have been given in section 1.4.3. From such information, Gerresheim (1973) mapped out twenty land regions (Figure 3.10) based on differences in vegetation. From this, it is clear that land region '14' to the south-east of the ecosystem represents a significant proportion of the total area on its own. This region consists largely of grassland and covers 10,000 km^2 of an area previously referred to as 'the plains'. The shear size and continuity of the area justifies considering it to be a zone in its own right.

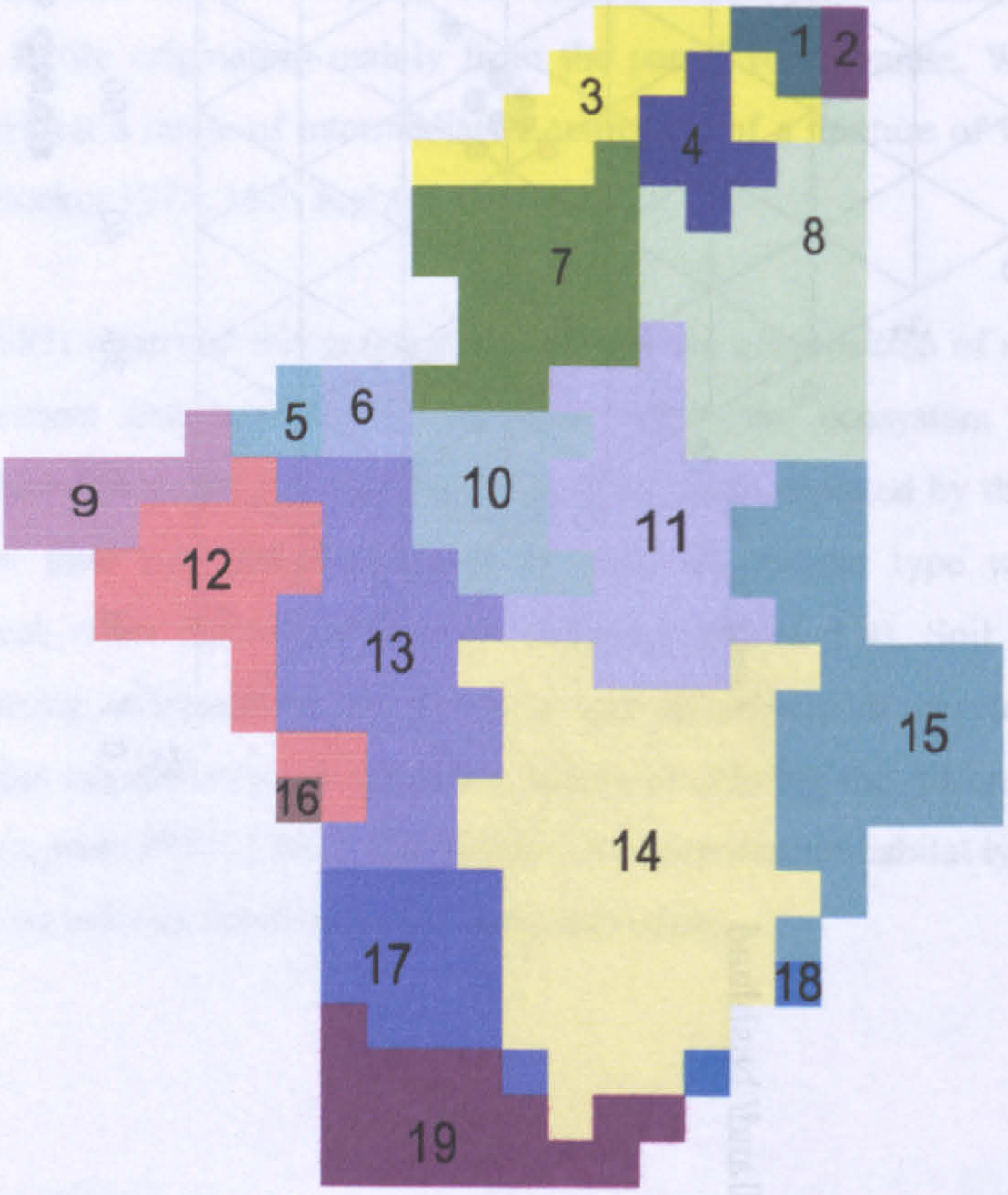

Figure 3.10 Map illustrating the twenty land regions in the Serengeti-Mara ecosystem proposed by Gerresheim (1973). Regions 3, 4, 6, 7,and 8 were regarded as the north, 9, 12 and 13 the west, 10 and 11 the central, and 14, 15 and 17 the plains (given in 30 by 30 m square plots; Gerresheim 1973; Pennycuick 1975).

It is more difficult to distinguish the other two areas by their vegetation. Both the western corridor and the northern extension are composed of a complex mosaic of habitat types, such as thorn-tree woodland, relict forest, bushland and grassland (Herlocker 1975). To ungulates this mosaic represents a number of feeding choices. The differential food quality between each habitat type strongly influences the regional distribution of these ungulates (Seagle & McNaughton 1992). It is therefore possible to use their specific seasonal distribution, particularly those of the migratory herbivores, as a guide to identify the other zones.

3.3.5 Migration patterns

The seasonal migration of wildebeest, plains zebra and Thomson's gazelle is without doubt the most studied aspect of the Serengeti-Mara ecosystem (Pearsall 1957; Swynnerton 1958; Grzimek & Grzimek 1960; Talbot & Stewart 1964; Watson 1967; Norton-Griffiths 1973; McNaughton 1983; Serneels & Lambin 2001). As a consequence, detailed information on the distribution of each of the migratory herbivores within the ecosystem during each season has been published (e.g. Watson 1967; von Frisch 1969; Schaller 1972; Pennycuick 1975; Maddock 1979). One particular investigation carried out by Bell (1969) provides data on the occupancy of 15 km^2 areas by each migrant for both seasons across the whole of the ecosystem. This data is illustrated in figures 3.11, 3.12 and 3.13, and shows that during the wet season all three migratory species reside within the plains region (see section 1.5.4). At the onset of the dry season, when the plains are unable to sustain such large concentrations of herbivores, the migrants move into the remainder of the ecosystem where they rely on the permanent supply of grass and water (McNaughton *et al.* 1989). Bell's (1969) data reveals that each migratory species relocates to a specific area within the ecosystem and this varies between species. For example, figure 3.13 shows that Thomson's gazelle move only as far as the lower half of the northern extension and eastern side of the western corridor (Norton-Griffiths *et al.* 1975). In contrast, both zebra and wildebeest move into the upper regions of the northern corridor and to the west of the western corridor, using the central regions as a migratory route, which according to Talbot & Talbot (1963), is a relatively quick transition. However, even in these areas there are differences in the distribution of these two species. The highest concentrations of zebra are found in the upper half of the northern extension, while more wildebeest are located along the western corridor. This is the occupancy early on in the dry season, although as Pennycuick (1975) reveals, wildebeest subsequently move into the upper half of the northern extension (Figure 3.14).

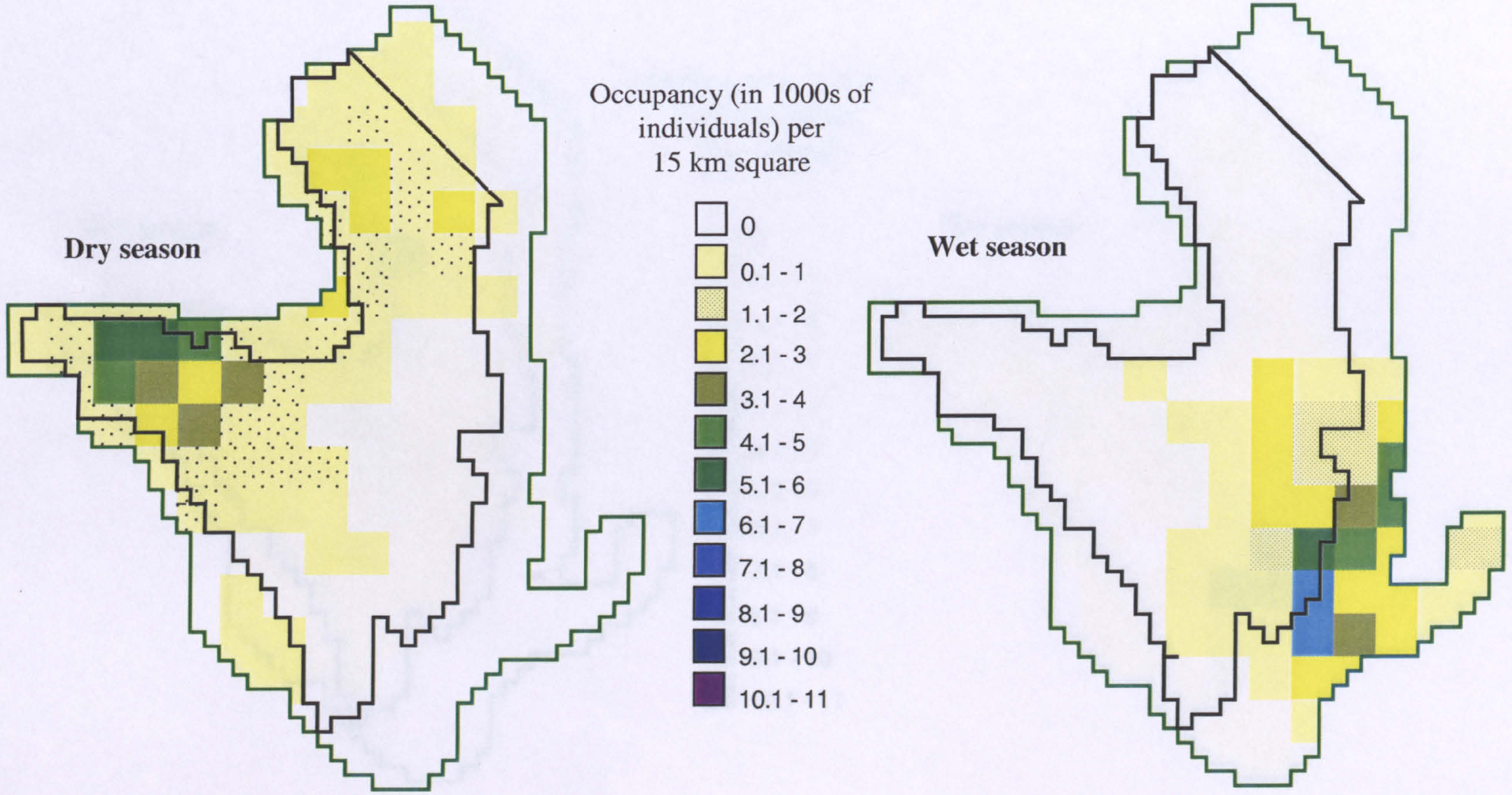

Figure 3.11 Seasonal occupancy per 225 km^2 of migratory wildebeest (*Connochaetes taurinus*) within the Serengeti-Mara ecosystem, illustrated using data from Bell (1969). The black outline indicates the border of the Serengeti National Park, and the green outline indicates the border of the ecosystem.

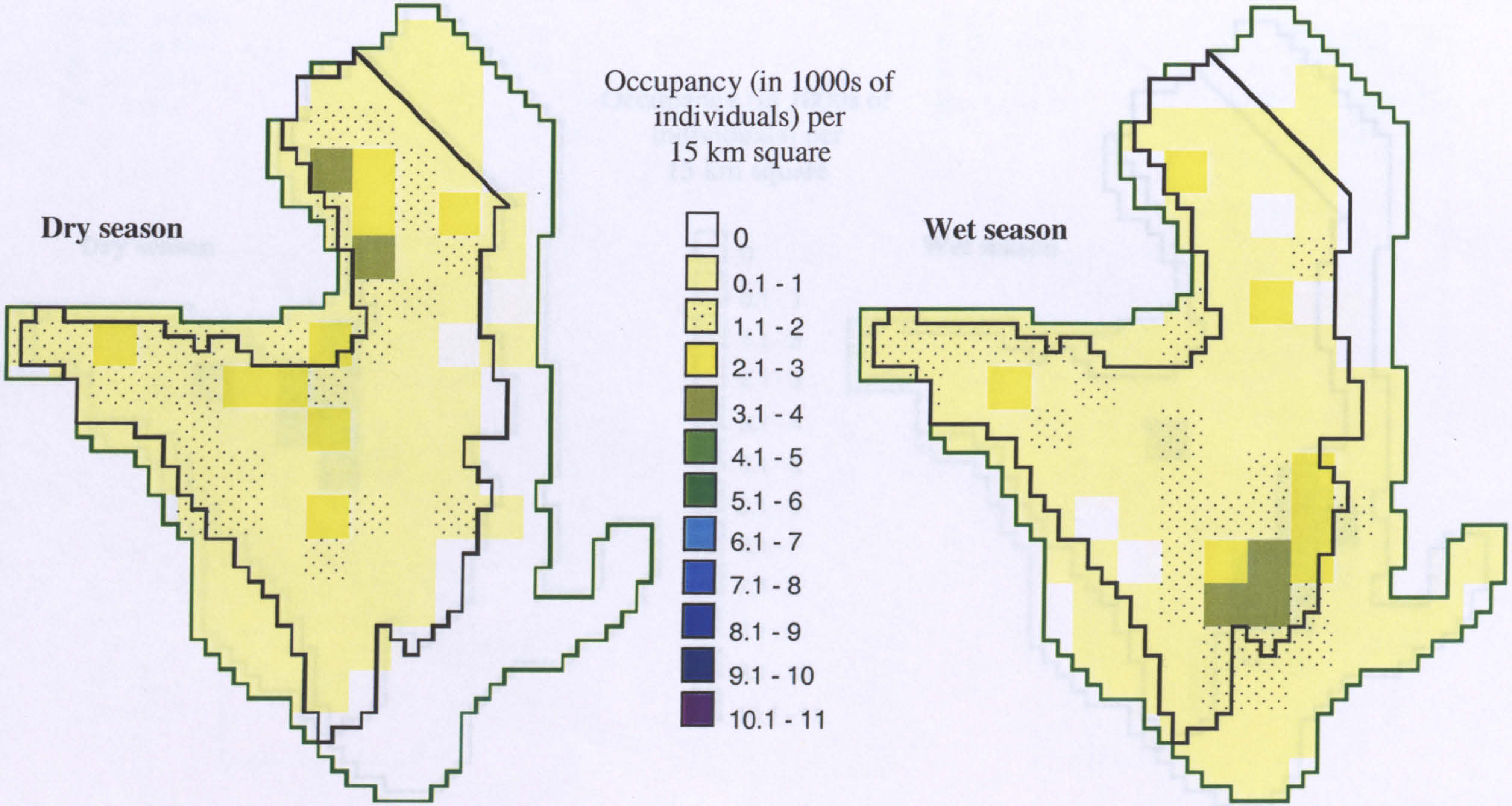

Figure 3.12 Seasonal occupancy per 225 km^2 of migratory zebra (*Equus burchelli*) within the Serengeti-Mara ecosystem, illustrated using data from Bell (1969). The black outline indicates the border of the Serengeti National Park, and the green outline indicates the border of the ecosystem.

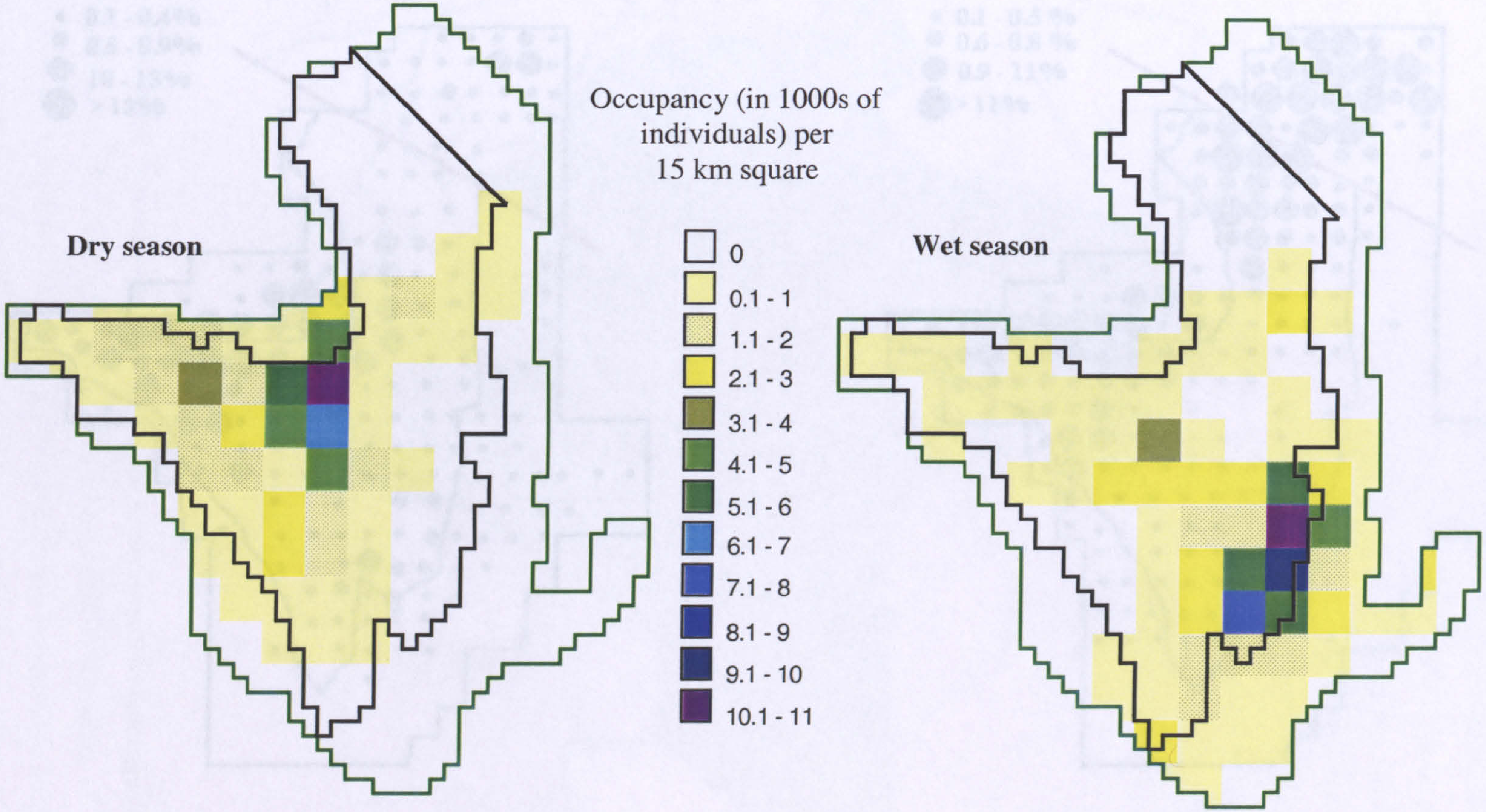

Figure 3.13 Seasonal occupancy per 225 km^2 of migratory Thomson's gazelle (*Gazella thomsoni*) within the Serengeti-Mara ecosystem, illustrated using data from Bell (1969). The black outline indicates the border of the Serengeti National Park, and the green outline indicates the border of the ecosystem.

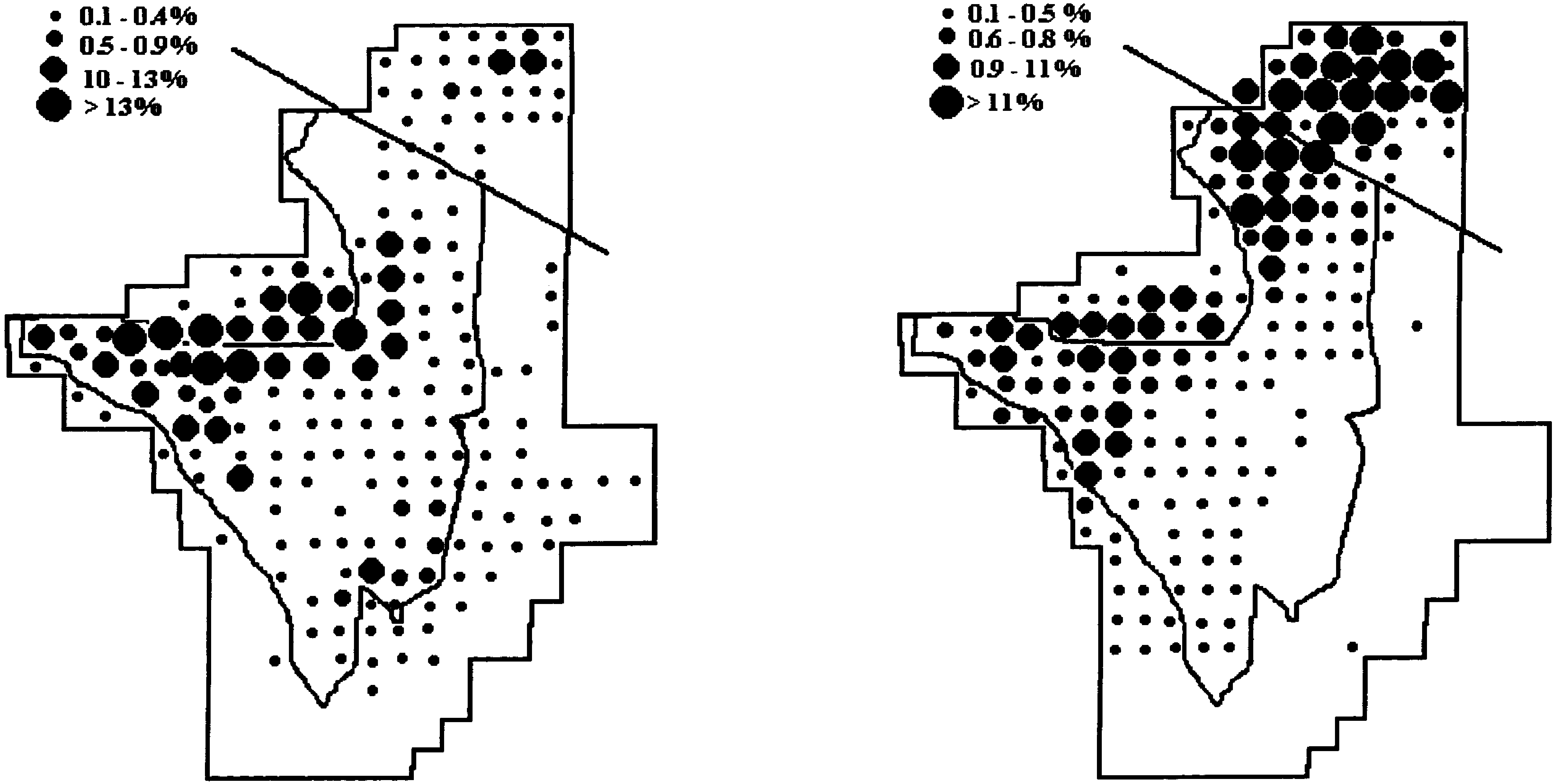

Figure 3.14 Wildebeest percentage occupancy (solid black circles) for May to July and August to November, respectively, within the Serengeti-Mara Ecosystem (solid black line) (Pennycuick 1975). The red line illustrates the Tanzania-Kenya border.

It is these distributions that define two further spatially separate regions within the Serengeti. Bell (1969) also identifies three equivalent zones and his interpretation of where the borders between these ecological regions lie is shown in figure 3.15.

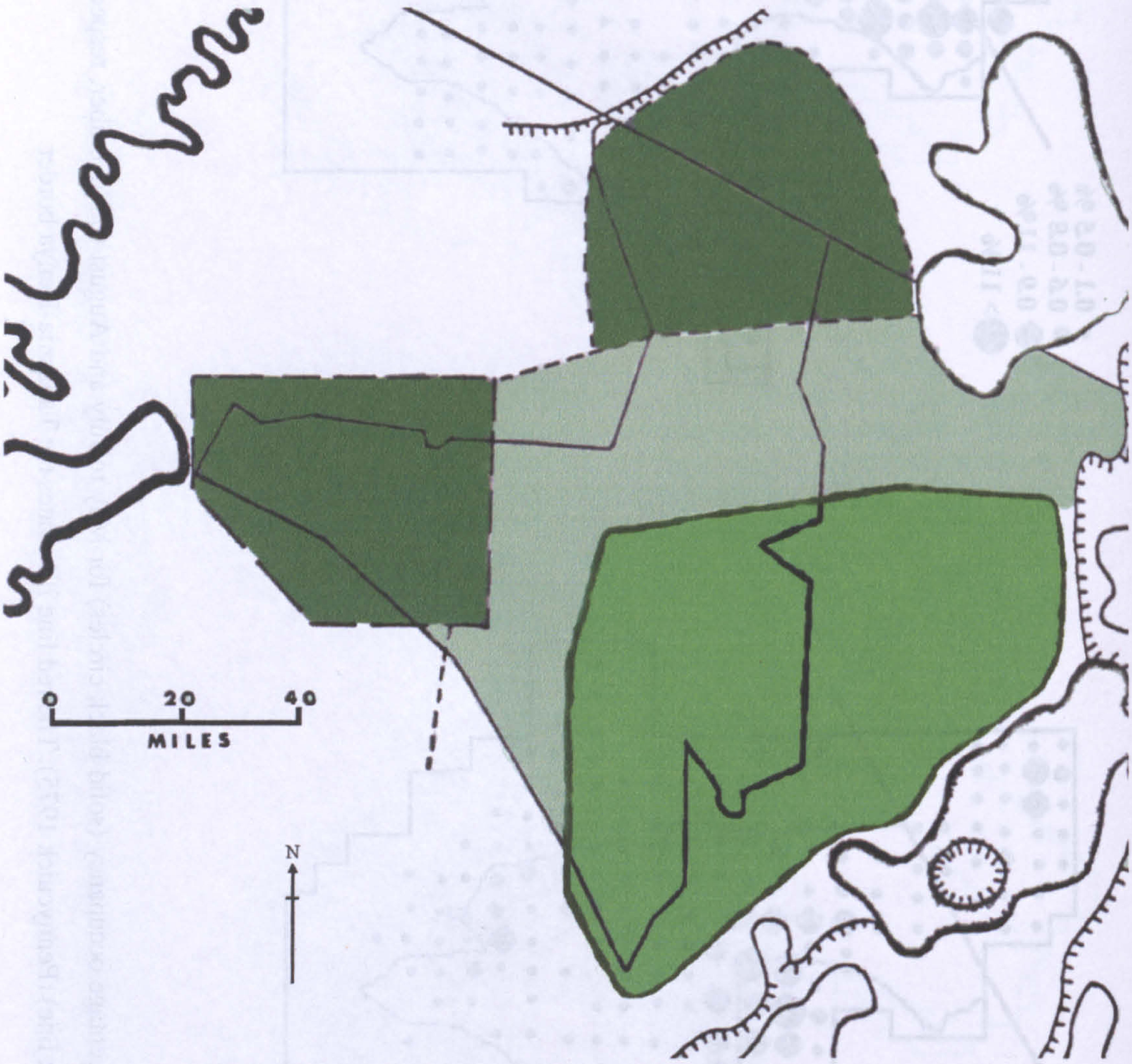

Figure 3.15 Map of suggested ecological zones of the Serengeti ecosystem by Bell (1969).

It is Bell's illustration that provides the basis on which the three spatial zones within the current model are defined. Using Gerresheim's (1973) mapped land regions as a template (shown in figure 3.10), more accurate borders can be created. These follow the boundaries of particular habitat types, rather then bisecting them. By doing this, specific habitats are allocated to a particular zone, as are the communities within them. As a result, the different species associated with these communities, and their interactions, can be more efficiently assigned to one particular sub-model. The final division of the ecosystem into 3 regions, spatially separate in aspects such as rainfall, geology, vegetation and species diversity are shown in figure 3.16.

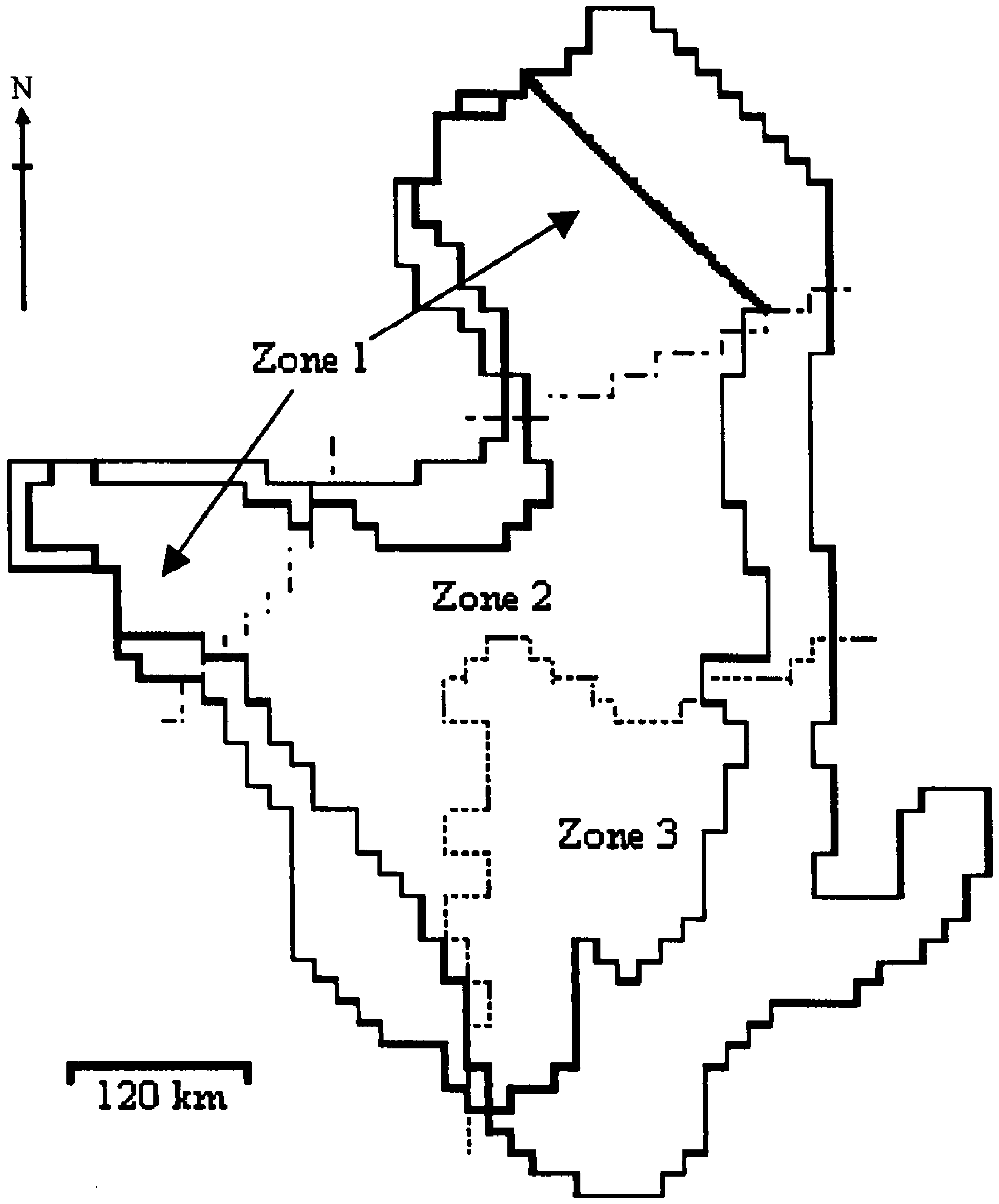

Figure 3.16 Map illustrating the three defined spatial divisions of the Serengeti-Mara ecosystem, as included in the model. The green outline indicates the border of the ecosystem, the black outline indicates the border of the Serengeti National Park, the dashed line shows the boundary between zone 1 and zone 2, and the dotted line shows the boundary between zone 3 and zone 2.

These zones are not equal in the area each covers. Zone 1 is the smallest, consisting of a portion of the upper northern extension and the arm of the western corridor, constituting an area of 8,450 km^2. Zone 3, representing the majority of the plains, covers 9,425 km^2. The largest, zone 2, incorporates 10,600 km^2 within the heart of the Serengeti.

3.4 SIX SUB-MODULES

From the three spatial zones and the two temporal zones discussed, a total of six sub-models are generated (Table 3.3). Within these module variations in rainfall and vegetation abundance, and species presence, can be adjusted to reflect the conditions and interactions specific to that zone and season. By combining the simulated data from each of the modules, a more accurate representation of the overall abundance of different populations within the ecosystem is produced.

Table 3.3 Six modules defined from spatial and temporal variations in the Serengeti-Mara ecosystem.

	Season	
Zone	Dry season zone 1	Wet season zone 1
	Dry season zone 2	Wet season zone 2
	Dry season zone 3	Wet season zone 3

CHAPTER 4: RAINFALL, GRASS GROWTH & GRASS AVAILABILITY

4.1 INTRODUCTION

After defining 6 modules, on which separate temporal and spatial scenarios within the Serengeti-Mara ecosystem could be modelled, the next stage is to introduce the ecosystem's components and variables.

In the Serengeti, the single most important variable affecting the whole ecosystem is rainfall (Braun 1973). It directly, or indirectly, influences every component (Cumming 1982; McNaughton & Georgiadis 1986). For instance, over a period of twenty years, McNaughton (1979a) observed that grass production depended primarily on rainfall, with the distribution of green biomass reflecting overall annual rainfall distribution (McNaughton 1985; Fryxell *et al.* 1988; Bell 1982; Boutton *et al.* 1988a; Seagle & McNaughton 1993; Mills *et al.* 1995). Hilborn & Sinclair (1979) further state that herbivore recruitment, mortality and migration are indirectly determined by rainfall through its effect on food availability (East 1984; Owen-Smith 1990; Pascual & Hilborn 1995). This correlation is most evident in the dry season, when rainfall is lowest and consequently food is limited (Braun 1973; Sinclair 1985; Wolanski *et al.* 1999).

Sinclair (1979c) suggests that rainfall can be used to predict primary production and thus herbivore numbers (McNaughton & Georgiadis 1986). However, he also acknowledges that larger herbivores do not consume the bulk of this primary production (Sinclair 1985). Other factors such as the maturation of grass, fire and both insect and small mammal herbivory, limit food availability (Bourlière & Hadley 1970; Walker *et al.* 1981; Gichohi *et al.* 1996; Homewood & Brockington 1999; du Toit & Cumming 1999). This additional off-take intensifies both intra- and inter-specific competition, within and between the large herbivore components, which in turn influences their population dynamics (Sinclair 1979c; Hilborn & Sinclair 1979; Sinclair 1985).

This chapter outlines how rainfall is included in the modules, its relationship with primary production, specifically grass growth, and the availability of grass as a basic resource to the large herbivore trophic level.

4.2 RAINFALL

Only annual rainfall data for zone 1 in the dry season is available for any length of time, given by Hilborn & Mangel (1997) (Table 4.1). However, it can be used as the basis to estimate rainfall for the remaining modules.

Table 4.1 Annual rainfall data for zone 1 in the dry season from 1960 to 1989 (Hilborn & Mangel 1997).

Year	Rainfall in mm for Zone 1 in the dry season	Year	Rainfall in mm for Zone 1 in the dry season
1960	100	**1975**	257
1961	38	**1976**	204
1962	100	**1977**	300
1963	104	**1978**	187
1964	167	**1979**	84
1965	167	**1980**	99
1966	165	**1981**	163
1967	79	**1982**	97
1968	91	**1983**	228
1969	77	**1984**	208
1970	134	**1985**	83
1971	192	**1986**	44
1972	235	**1987**	112
1973	159	**1988**	191
1974	211	**1989**	202

Seasonal rainfall figures over a few years in each zone in the present model are taken from Pennycuick (1975). She allocated seasonal rainfall measurements to each of the land regions that Gerresheim (1973) identified within the Serengeti ecosystem (section 3.3.4). The seasonal rainfall for each zone can then be estimated by taking an average of those measurements for regions within a particular zone (Table 4.2).

Table 4.2 Average rainfall in millimetres for each of the six modules between 1962 to 1972, taken from Pennycuick (1975).

Zone (present model)	Land Region (Pennycuick 1975)	Rainfall in the wet season (mm)	Average wet season rainfall (mm)	Rainfall in the dry season (mm)	Average dry season rainfall (mm)
1	3	862	**818**	255	**212**
	4	806		251	
	7	802		244	
	8	867		175	
	9	751		172	
	12	820		176	
2	10	641	**723**	165	**138**
	13	662		128	
	11	743		159	
	17	844		99	
3	14	511	**565**	79	**85**
	15	619		91	

The bold figures in table 4.2 can, therefore, be used to calculate the relative difference between the rainfall in zone 1 in the dry season (set at 1.00), and the other five modules (Table 4.3).

Table 4.3 Average rainfall in millimetres for each module (Table 4.2) and their relative magnitudes compared with zone 1 in the dry season.

	Zone 1	Zone 2	Zone 3
Wet season	818	723	563
Relative difference	*3.75*	*3.32*	*2.65*
Dry season	212	138	85
Relative difference	*1.00*	*0.63*	*0.39*

Hilborn & Mangel's (1997) annual rainfall data for zone 1 in the dry season (Table 4.1) can then be multiplied by each relative difference (Table 4.3), thus estimating the annual rainfall for each of the other modules (Figure 4.1). Note that a major increase in annual rainfall during the mid-1970s, as discussed in section 2.3.2, is clearly visible in figure 4.1.

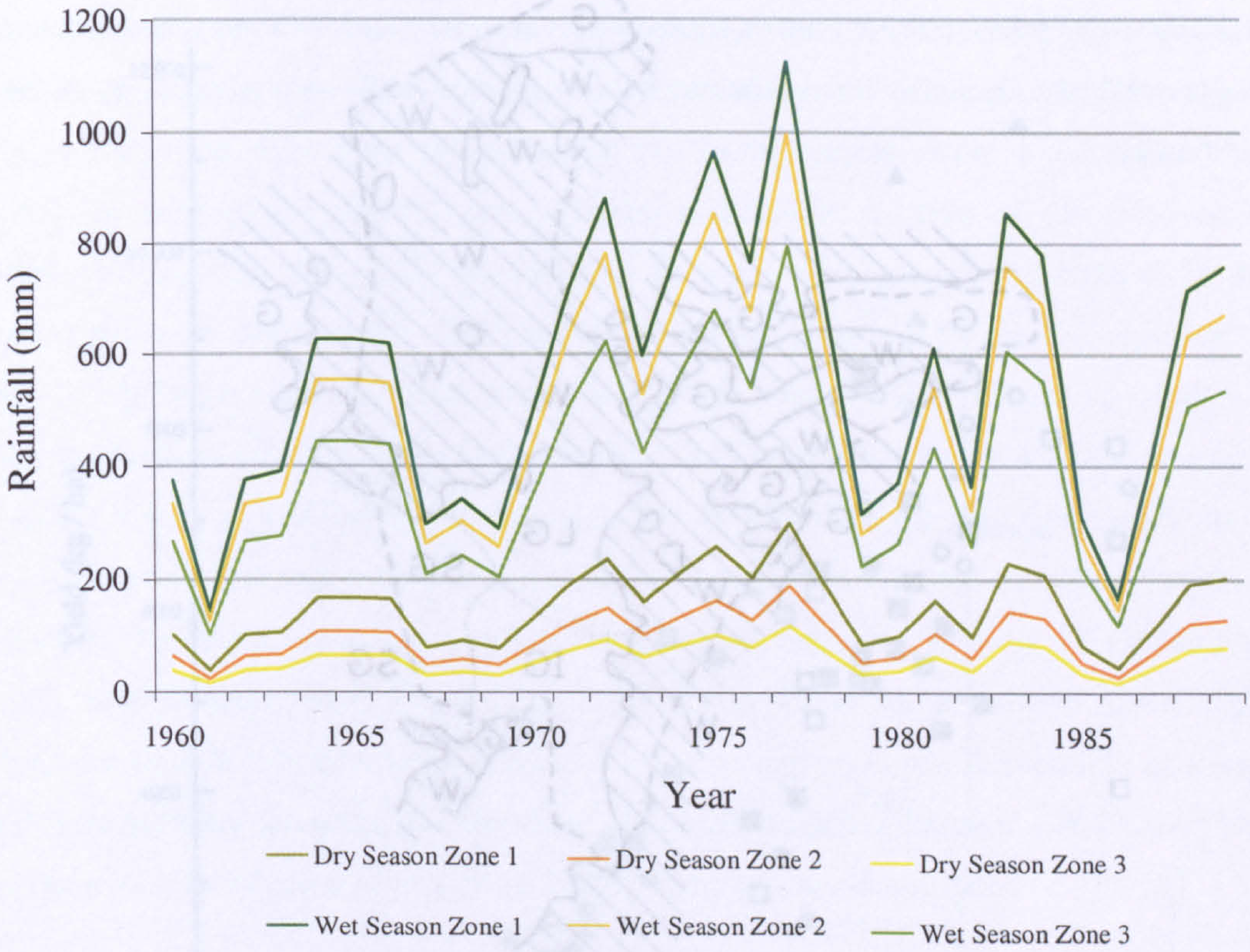

Figure 4.1 Annual rainfall in millimetres for each module of the Serengeti-Mara ecosystem from 1960 to 1989.

4.3 GRASS GROWTH

The next stage of the model was to estimate annual grass production from the rainfall data. Deshmukh (1984) confirmed a highly significant correlation ($P<0.001$) between peak biomass and precipitation, when he combined studies carried out across East and southern Africa, although considerable variation did exist. He concluded that only grass production and rainfall data from a specific area would reveal a realistic relationship. There are two known studies where such measurements were collected within the Serengeti-Mara ecosystem. These are investigations carried out by Braun (1973) and Sinclair (1975). In Braun's study, data was collected between 1966 and 1972 from enclosure plots set up on selected sites in long, intermediate and short grassland on the plains, as well as sites in the woodlands (Figure 4.2).

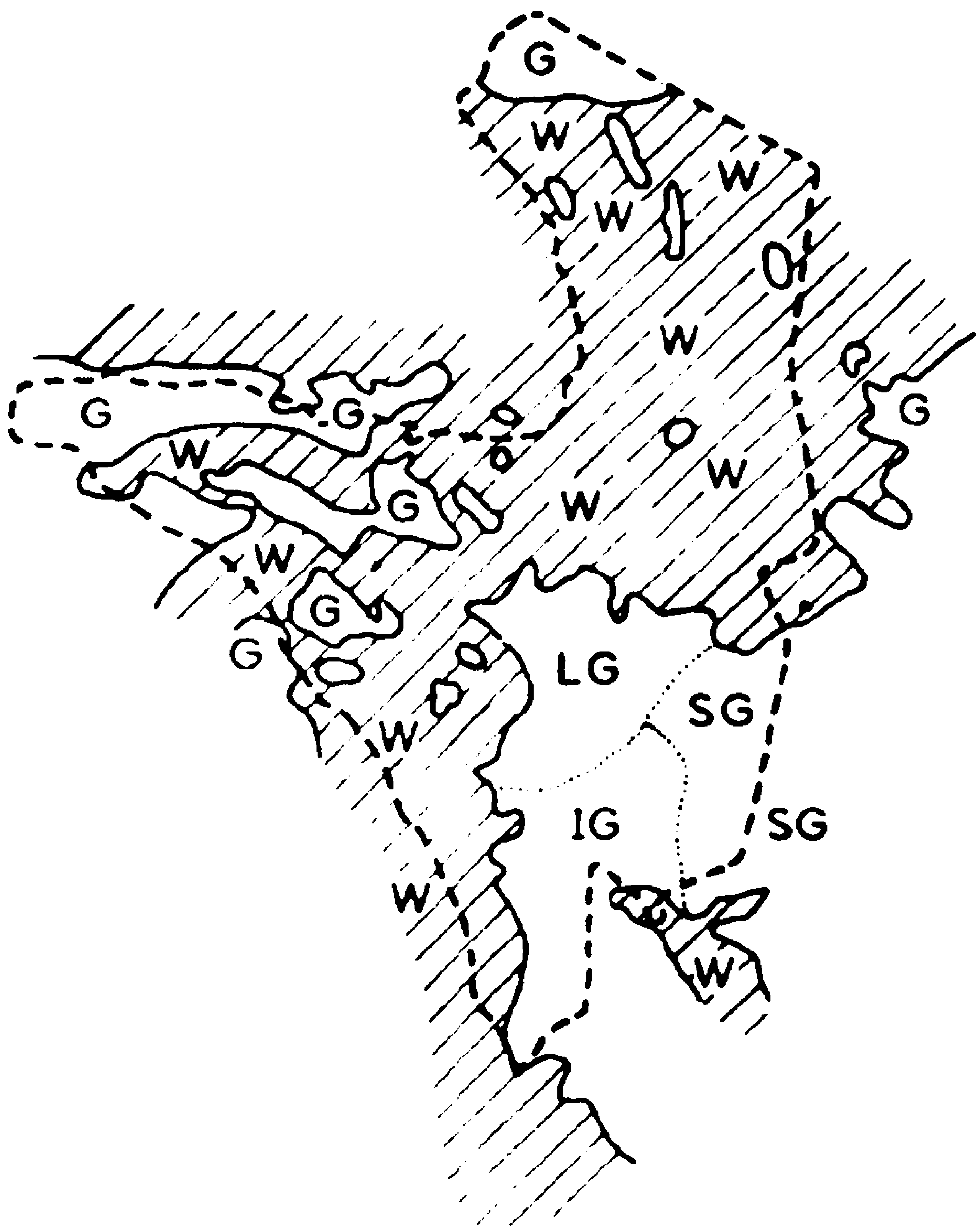

Figure 4.2 The distribution of grassland (G) and woodland (W) in the Serengeti-Mara ecosystem. The approximate boundaries between the short (SG), intermediate (IG) and long grassland zones (LG) within the Serengeti plains are indicated by a dotted line (Braun 1973).

The enclosure plots varied between 4 and 25 m^2 and a number of grass samples, between 0.25 and 1 m^2, were clipped from each plot. The amount of primary production within these enclosures was determined from this clipping and rainfall was measured from nearby storage gauges. Braun (1973) simply plots all his results together, and discusses any trends he observed (Figure 4.3). He states that the data points show that with increasing rainfall, the production per millimetre of rainfall (the yield/rainfall quotient: YRQ) also increases. He further notes that every vegetation type has its own relationship with rainfall (Belsky 1985).

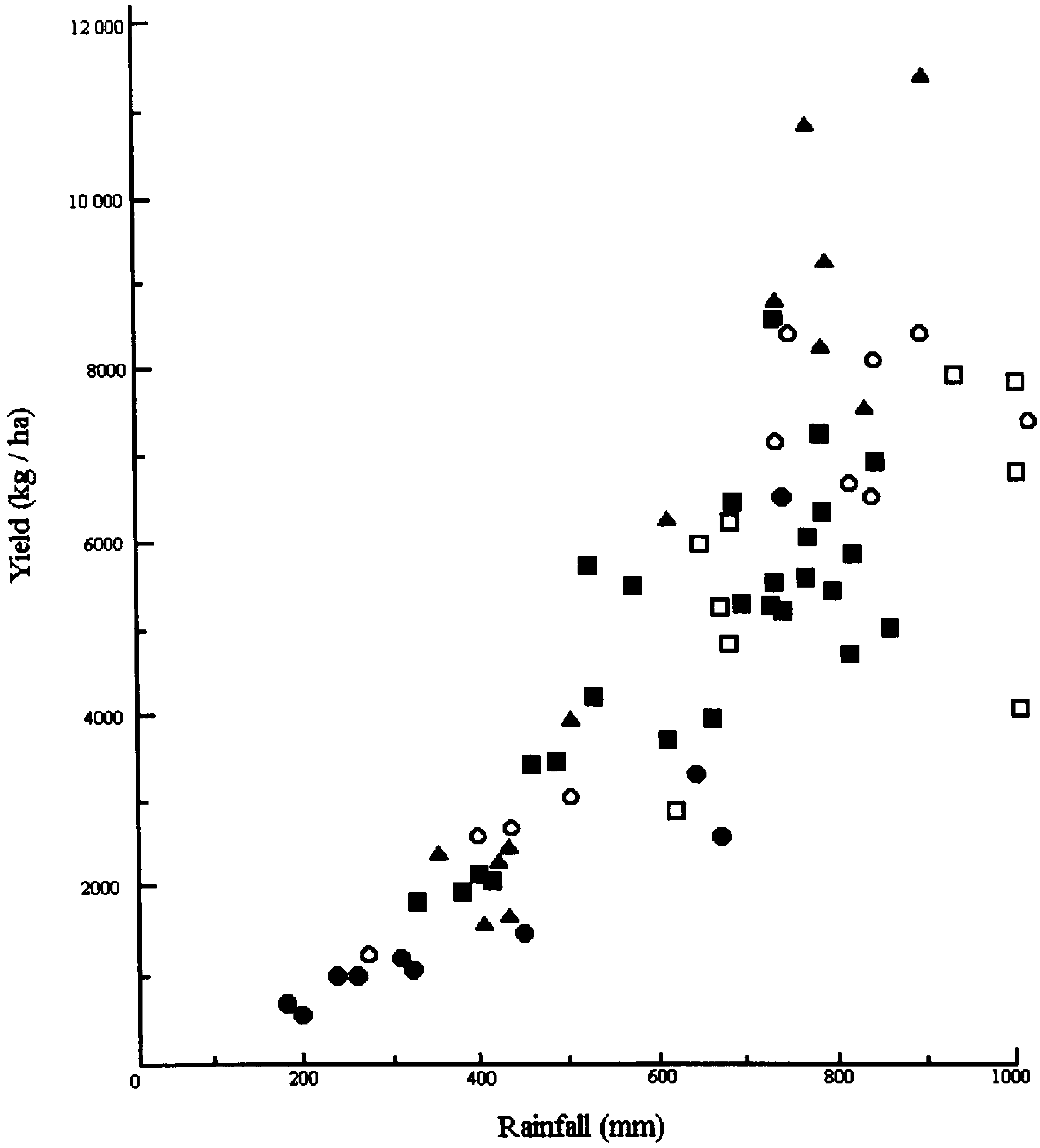

Figure 4.3 Grass yield on sites in the short grassland (black dots), the intermediate grassland (black triangles for *Andropogon greenwayi* stands and circles for mixed stands), the long grassland (black squares) and the woodland zone (open squares) with increasing rainfall in millimetres (Braun 1973).

Sinclair (1975), on the other hand, goes one step further. Using the grass growth and rainfall data collected by Braun (1973) in conjunction with data collected in his own research using a similar method to Braun's, Sinclair attempted to find the relationship between grass growth and rainfall.

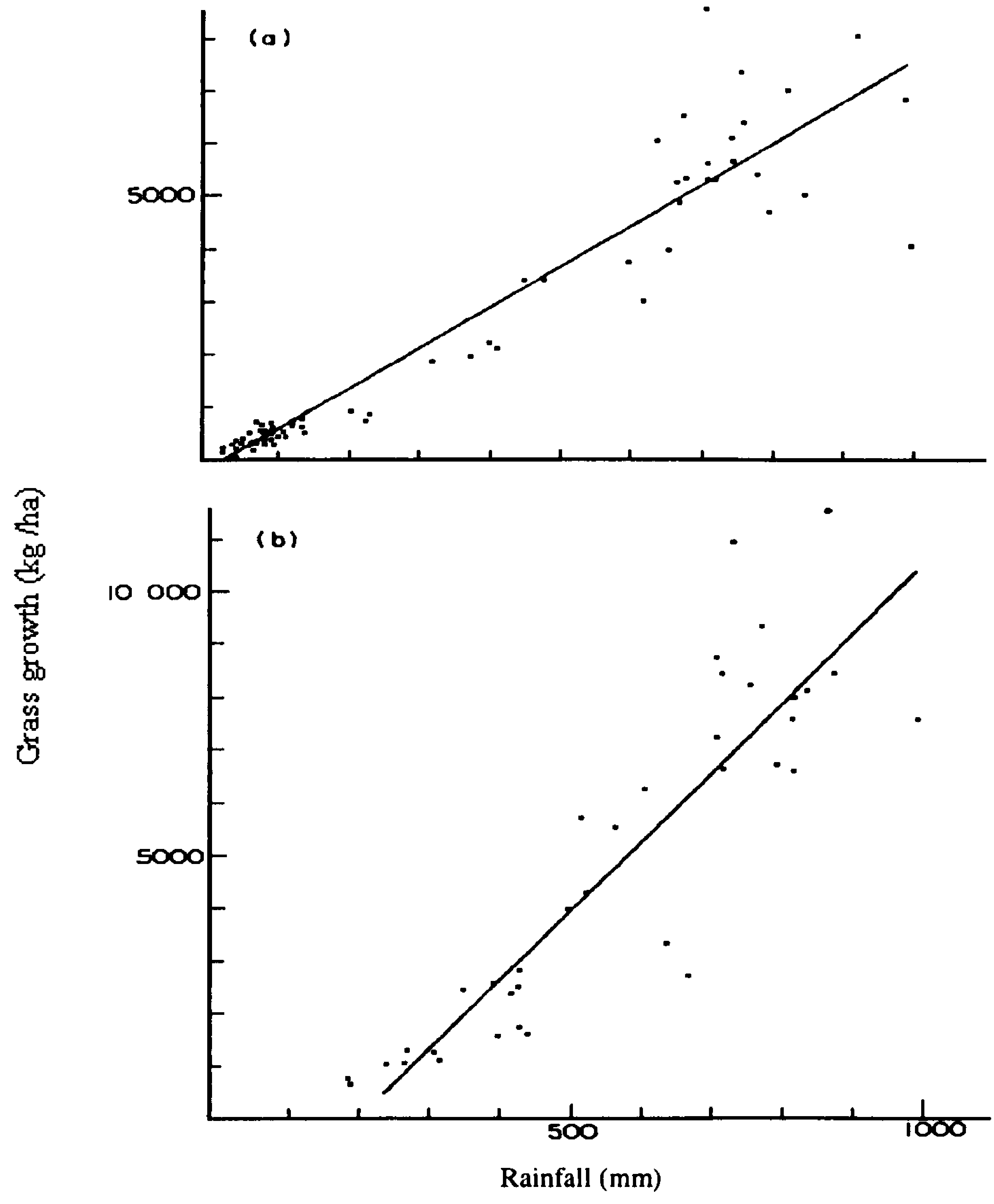

Figure 4.4 The regressions describing the relationship between dry weight grass production (y) and rainfall during the period of growth, a) long grassland, where $y = 7.6719x - 201.85$ and b) short grassland, where $y = 12.88x - 2494.9$ (Sinclair 1975).

Sinclair concluded from his investigation that a linear model correctly represented this relationship. Figure 4.4 illustrates the linear regression line he found to best fit the relationship between these two variables. However, this relationship specifically relates to long grassland and short grassland independently. In the current model, a regression line is needed for each of the general grassland types described in each of the six modules. Therefore, to reveal the specific relationship between grass growth and rainfall in each module, different combinations of Braun and Sinclair's data can be used to represent the relevant vegetation types found in each. For example, since zone 3 is made up of all three types of grassland (short, intermediate and long), as illustrated in figure 4.2 (also refer back to section 1.4.3), a combination of these data points is used in the modules specific to this zone. Furthermore, as both zone 1 and 2 contain long grass species and are within the bounds of the woodland sites, the data points for both these can, therefore, be used. This gives a total of 102 measurements used to calculate the regression line for grass production against rainfall for zone 3 (a combination of 43 of Sinclair's long grassland data and 59 of Braun's short, intermediate and long grassland data) and 76 data points for zones 1 & 2 (using all of Sinclair's long grassland data and 33 of Braun's long and woodland data).

This data was then analysed using a regression curve estimation (SPSS 1998). Various regression models were fitted, including linear, logarithmic, S, compound, growth, logistic, cubic, exponential and quadratic. Furthermore, each of these models were also fitted both with constants and without (where the y intercept = 0). R^2, the coefficient of determination, was used to test goodness of fit, and F values for each model were used to identify whether a significant amount of variation in y is explained by x (see tables 4.4 to 4.7). In the present model, the closer the R^2 value to 1, the greater the similarity between grass growth variability and rainfall variability, and the better fit the regression model to the data (Sokal & Rohlf 1995).

Table 4.4 Results of fitting regression curve models with constants (b_o) for dry weight grass production against rainfall, in zone 3 (Braun 1973). Note that F values are significant, as *P<0.05*

			Coefficients for regression model			
Regression model	R^2	F	b_0	b_1	b_2	b_3
Linear	0.824	467.32	-574.18	8.95		
Logarithmic	0.645	181.66	-8977.60	2166.75		
Inverse	0.312	45.29	4247.74	-171776		
Quadratic	0.847	274.04	121.49	2.55	0.007	
Cubic	0.851	186.50	526.33	-3.75	0.025	-1.E-05
Compound	0.826	474.27	277.77	1.00		
Power	0.877	712.06	2.3	1.17		
S	0.640	177.47	8.13	-113.79		
Growth	0.826	474.24	5.63	0.004		
Exponential	0.826	474.24	277.77	0.004		
Logistic	0.826	474.24	0.004	1		

Table 4.5 Results of fitting regression curve models without constants (*b_o*) for dry weight grass production against rainfall, in zone 3 (Braun 1973). * indicates F values that are not significant, as *$P>0.05$*

			Coefficients for regression model			
Regression model	R^2	F	b_0	b_1	b_2	b_3
Linear	0.902	925.08	0	8.03		
Logarithmic	0.633	174.25	0	593.48		
Inverse	0.015	1.56*	0	41021		
Quadratic	0.921	580.18	0	3.18	0.007	
Cubic	0.921	385.80	0	1.60	0.013	-5.E-06
Compound	0.772	341.09	0	1.01		
Power	0.995	20623.2	0	1.30		
S	0.249	33.48	0	293.43		
Growth	0.772	341.09	0	0.01		
Exponential	0.772	341.09	0	0.01		
Logistic	0.772	341.09	0	0.99		

Table 4.6 Results of fitting regression curve models with constants (*b_n*) for dry weight grass production against rainfall, in zone 1 & 2 (Braun 1973; Sinclair 1975). Note that F values are significant, as $P<0.05$.

			Coefficients for regression model			
Regression model	R^2	F	b_0	b_1	b_2	b_3
Linear	0.913	790.81	-208.94	11.66		
Logarithmic	0.798	296.19	-7863.70	5078.60		
Inverse	0.414	52.90	4026.04	-2.E+06		
Quadratic	0.913	390.71	-244.21	9.25	4.E-04	
Cubic	0.929	318.98	468.35	-18.42	0.028	-2.E-05
Compound	0.821	343.24	272.59	1.00		
Power	0.905	715.72	2.53	1.7		
S	0.676	156.69	8.10	-686.99		
Growth	0.821	343.24	5.61	0.003		
Exponential	0.821	343.24	272.59	0.003		
Logistic	0.821	343.24	0.004	1		

Table 4.7 Results of fitting regression curve models without constants (b_o) for dry weight grass production against rainfall in zone 1 & 2 (Braun 1973; Sinclair 1975). * indicates F values that are not significant, as $P>0.05$

			Coefficients for regression model			
Regression model	R^2	F	b_0	b_1	b_2	b_3
Linear	0.954	1561.17	0	7.38		
Logarithmic	0.669	153.65	0	547.42		
Inverse	0.015	1.14*	0	-30723.40		
Quadratic	0.954	776.82	0	6.76	8.E-04	
Cubic	0.961	612.75	0	2.01	0.17	-1.E-05
Compound	0.715	190.26	0	1.01		
Power	0.995	16389.6	0	1.32		
S	0.286	30.38	0	267.68		
Growth	0.715	190.26	0	0.01		
Exponential	0.715	190.26	0	0.01		
Logistic	0.715	190.26	0	0.99		

From an examination of the R^2 and F values, the regression model that best fits the grass growth/rainfall data, for all modules is the power model without a constant (Figure 4.5 & 4.6). Both R^2 values are very high at 0.995.

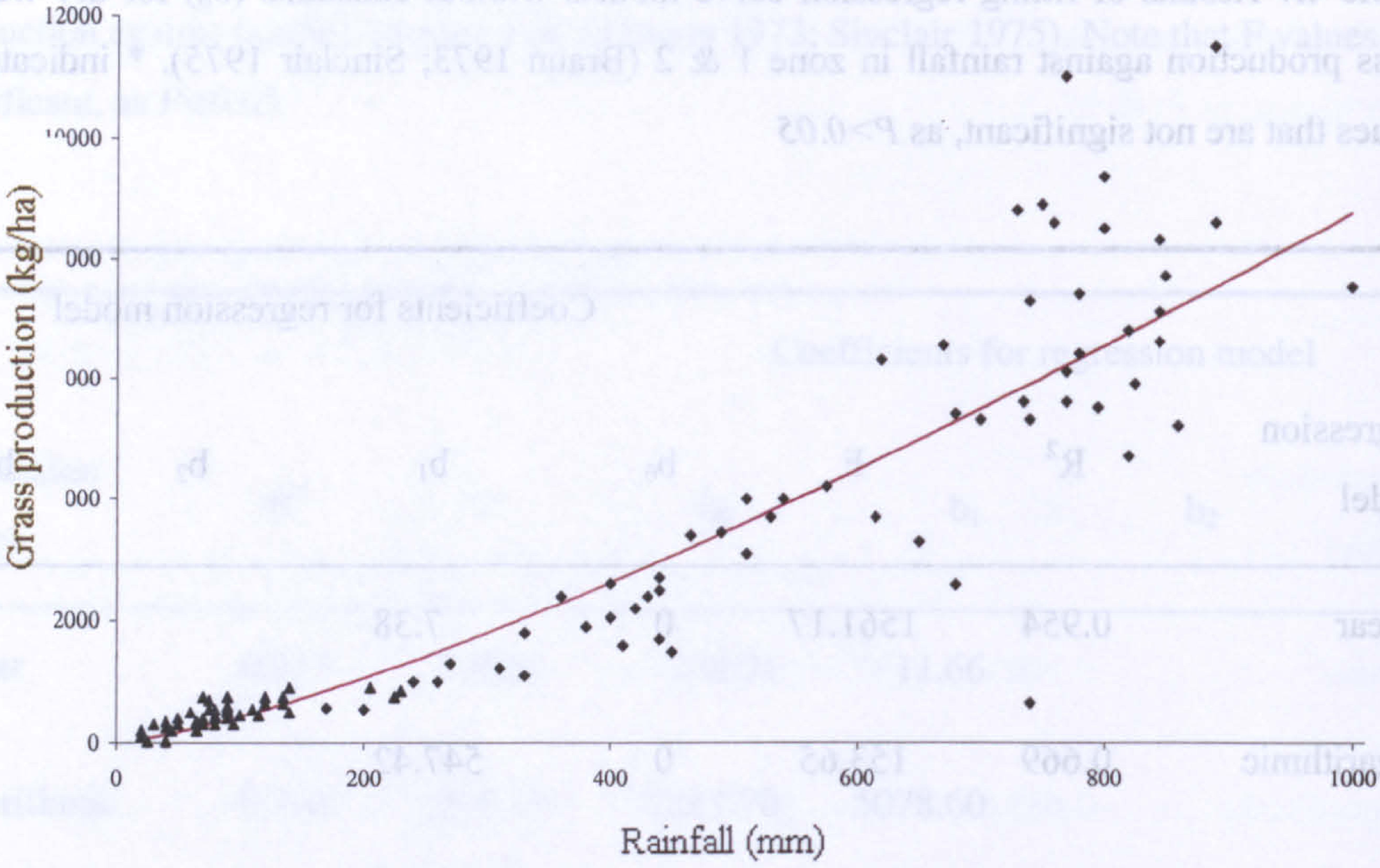

Figure 4.5 Graph illustrating Braun's (1973) (diamonds) and Sinclair's (1975) (triangles) data for rainfall in millimetres and grass yield in kilograms of dry matter per hectare for the zone 3. Red line illustrates the relationship between the two as represented by the power model ($y = x^{(b1)}$).

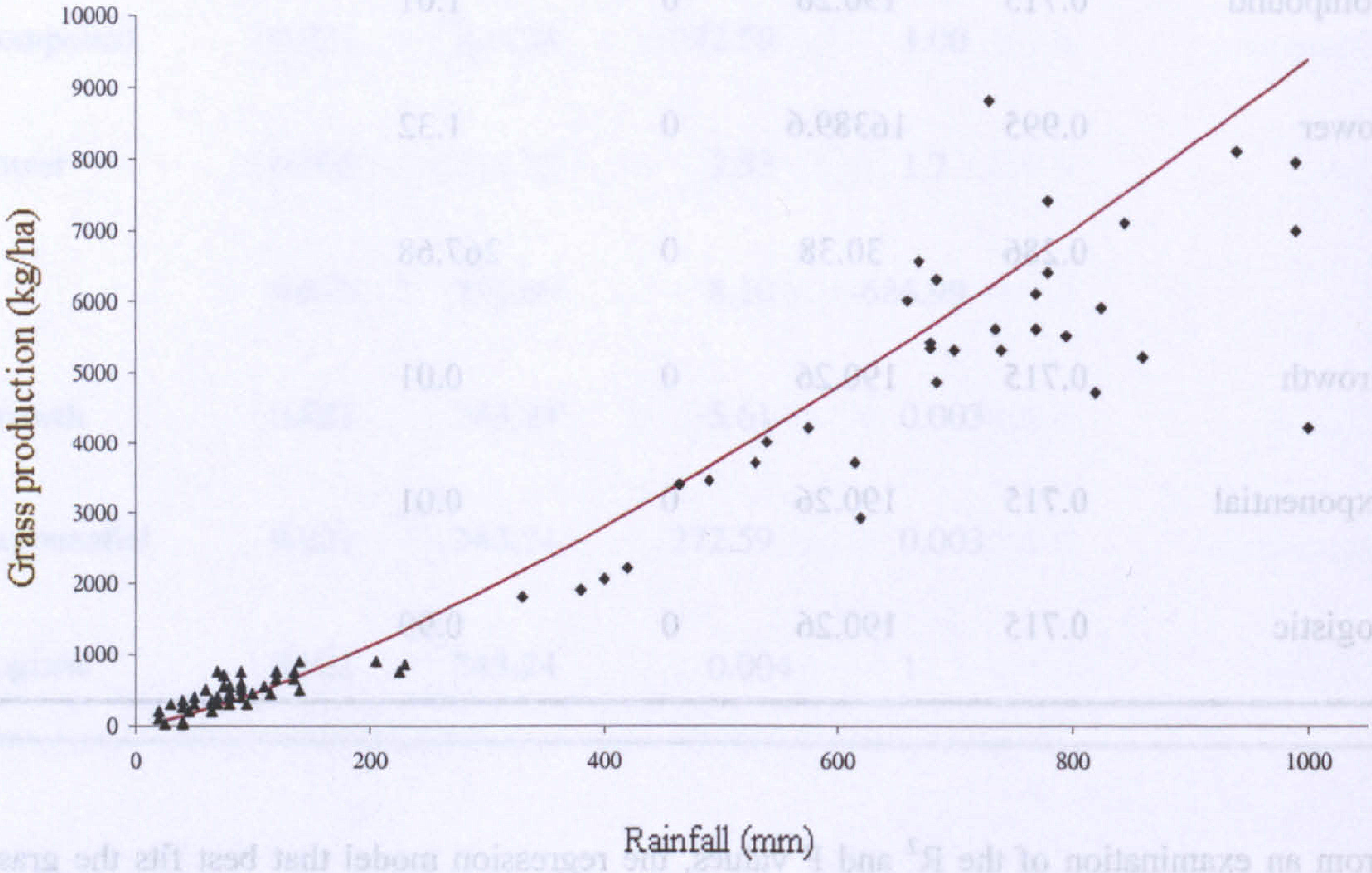

Figure 4.6 Graph illustrating Braun's (1973) (diamonds) and Sinclair's (1975) (triangles) data for rainfall in millimetres and grass yield in kilograms of dry matter per hectare for zones 1 & 2. Red line illustrates the relationship between the two as represented by the power model ($y = x^{(b1)}$).

Of course, continued increases in rainfall would not necessarily continue to give more grass. Realistically, a continued increase in the amount of rainfall may have no further effect on the amount of grass grown, and may even be detrimental, leading to water logged soil and oxygen starved roots. However, Seagle & McNaughton (1993) state that physically the soils are not conducive to water logging, but the extent to which run-off occurs does limit the amount of rainfall available to grass (Pearsall 1957; Figure 4.7).

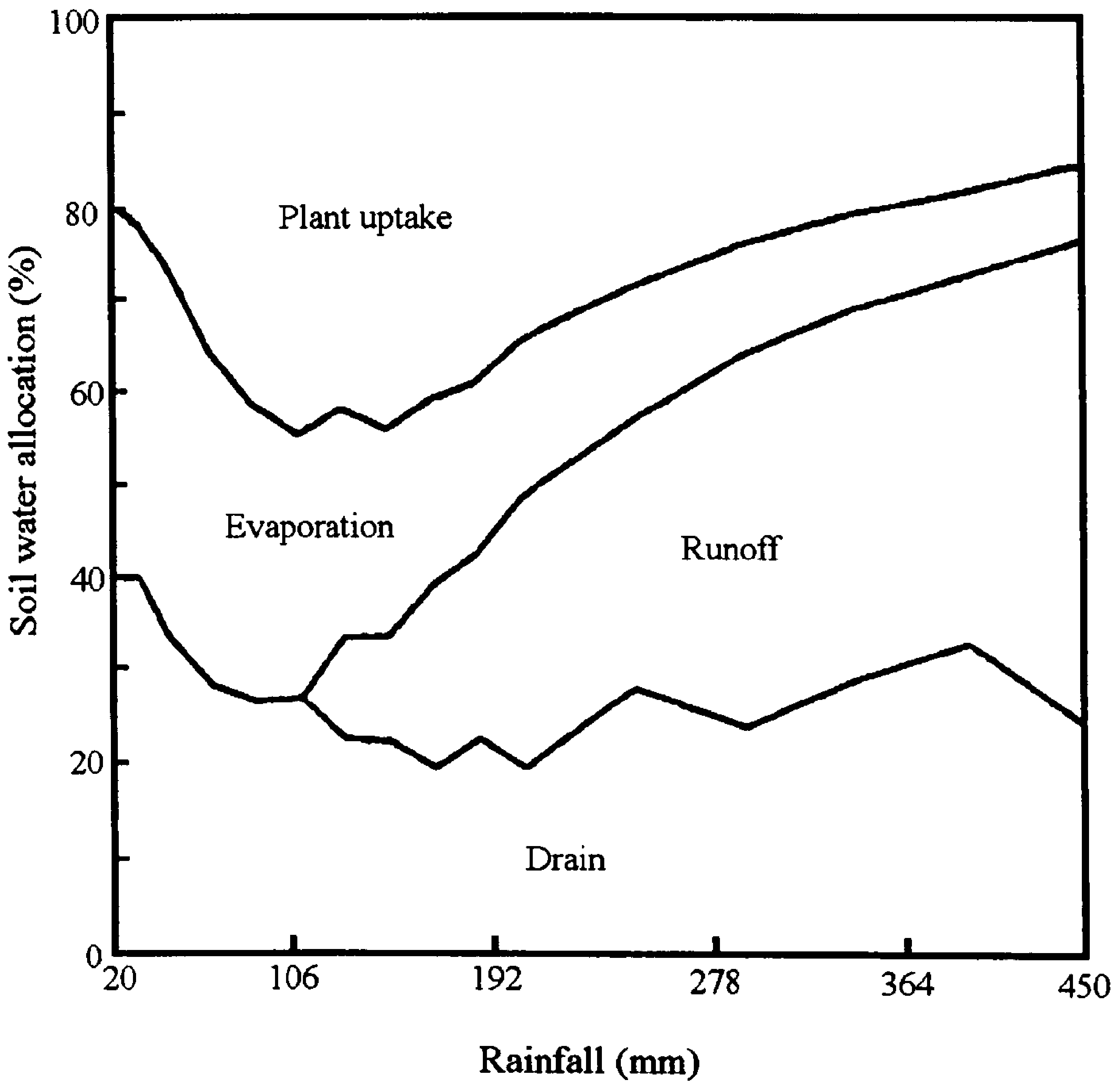

Figure 4.7 Illustration of the allocation of rainfall to the soil (Seagle & McNaughton 1993).

In the present context, this is of little importance as there is a limit to the amount rainfall that could fall on the Serengeti-Mara ecosystem. For example, in Braun's (1973) investigation the maximum rainfall value was 1000 mm and the data best fits a power model to this point. In the present model the maximum rainfall estimated is 1125 mm (Table 4.1) and it was assumed this increase would not change the shape of the model significantly. The power model can, therefore, be accepted as the most accurate representation of the relationship between grass growth and rainfall for the different modules.

The coefficients (b_l) for each power model can then be used in the following equation,

$$G = R^{(b_1)} \tag{4.1}$$

where R is rainfall (millimetres), b_l is the power model coefficient (Table 4.5 & 4.7) and G the resulting green grass production (dry matter in a kilogram). This equation was then incorporated into each module, using the appropriate rainfall data and power coefficients, in order to calculate the amount of green grass annually grown in each. The equations used for zone 3 and zones 1 & 2, respectively, were;

$$G = R^{(1.3033)} \tag{4.2}$$

$$G = R^{(1.3242)} \tag{4.3}$$

The resulting seasonal grass production data (kilograms per hectare) from 1960 to 1989 for each module is shown in figure 4.8, in which a pattern very similar to that of the rainfall in figure 4.1 can be seen.

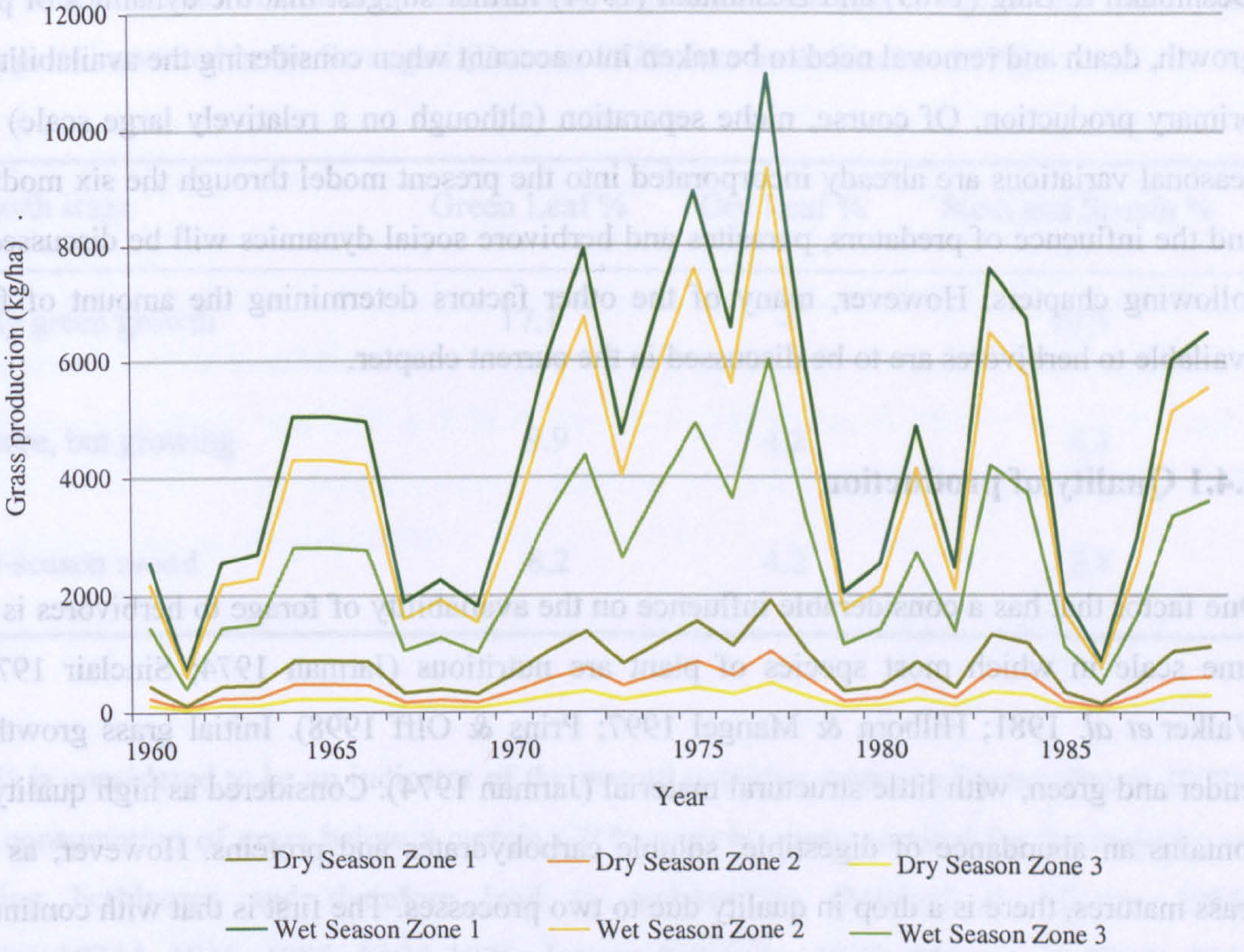

Figure 4.8 Annual green grass production in dry matter in kilograms per hectare for each module of the Serengeti-Mara ecosystem from 1960 to 1989.

4.4 GRASS AVAILABILITY

As previously suggested in section 4.1, it is recognised that herbivores only consume a certain proportion of primary production (Wiegert & Evans 1967; de Vos 1969; Bourlière & Hadley 1970; Braun 1973; Phillipson 1973; Strugnell & Pigott 1978; Owaga 1980; Sinclair 1985; Deshmukh 1986; Onyeanusi 1989; Gichohi *et al.* 1996; du Toit & Cumming 1999). Consequently, there has been continuing controversy whether food resources, predators, weather extremes or social interactions control herbivore populations (Jarman 1974; Sinclair 1974d; Owen-Smith 1990). Hairston *et al.* (1960) and Slobodkin *et al.* (1967) argue that these restrained levels of consumption support the hypothesis that the herbivore trophic level is not food limited, but instead limited by predators and parasites. However, Sinclair (1985) points out that this precludes competition, niche separation, seasonal variations and other factors that cause fluctuations in resource available.

Deshmukh & Baig (1983) and Deshmukh (1984) further suggest that the dynamics of plant growth, death and removal need to be taken into account when considering the availability of primary production. Of course, niche separation (although on a relatively large scale) and seasonal variations are already incorporated into the present model through the six modules and the influence of predators, parasites and herbivore social dynamics will be discussed in following chapters. However, many of the other factors determining the amount of food available to herbivores are to be discussed in the current chapter.

4.4.1 Quality of production

One factor that has a considerable influence on the availability of forage to herbivores is the time scale in which most species of plant are nutritious (Jarman 1974; Sinclair 1974d; Walker *et al.* 1981; Hilborn & Mangel 1997; Prins & Olff 1998). Initial grass growth is tender and green, with little structural material (Jarman 1974). Considered as high quality, it contains an abundance of digestible, soluble carbohydrates and proteins. However, as the grass matures, there is a drop in quality due to two processes. The first is that with continued growth, there is an increase in structural tissues containing large amounts of insoluble lignin, cellulose and hemicellulose (Afolayan & Fafunsho 1978; Jarman 1974; Jarman & Sinclair 1979; Bell 1982; McNaughton & Georgiadis 1986; Prins & Olff 1998; Ritchie & Olff 1999). The second is that the abundance of nutrients in leaves is reduced, as soluble constituents are withdrawn to the grass roots, where they are stored (Sinclair 1974; Jarmen & Sinclair 1979). A consequence of both these processes is that grass becomes old and tough over a certain period of time. A chemical analysis of grass during this time, shows that the decline in the quality of grass corresponds with a decline in the percentage of crude protein (*CP*) it contains (Braun 1973; Duncan 1975; Jarman & Sinclair 1979; van Soest 1982; Fryxell 1991; Table 4.8). Table 4.8, also shows that *CP* % differs between the various plant structures. For example, both stems and sheath have only half the *CP* % of leaves.

Table 4.8 Examples of crude protein content, expressed as a percentage of dry matter, of grass parts harvested in the Serengeti (Duncan 1975; Jarman & Sinclair 1979).

Growth stage	Green Leaf %	Dry Leaf %	Stem and Sheath %
Early green growth	17.1	-	10.3
Mature, but growing	9.9	4.2	4.1
Dry-season sward	8.2	4.2	2.8

CP % is considered to be an indicator of the overall nutritive content of grass (Braun 1973). The consumption of grass below a certain *CP* %, may be uneconomical for the majority of grazing herbivores and therefore lead to malnutrition (Milford & Minson 1966; Sinclair 1974d, 1975, 1985; Field 1976; Jarman & Sinclair 1979; Moe *et al.* 1990). This threshold occurs when grass contains below 4 % *CP* (Bredon & Wilson 1963; Milford & Minson 1966; Sinclair 1975, 1977b, 1985; Field 1976; Jarman & Sinclair 1979; Owen-Smith 1982; Boutton *et al.* 1988b). Consequently, in the present model grass above this level is referred to as 'green grass' and below it grass is referred to as 'dry grass'. One implication of this maturation is that there may be a standing crop of grass present in an area, but it is not necessarily available to the majority of herbivores (Sinclair 1975; Edroma 1984). This further implies that many of the components in the model must specifically select for green grass when foraging. In reality, selectivity may be more sophisticated than this simple choice. For instance, it is well documented that inter-specific competition within any ecosystem is reduced by components following specific foraging criteria (Lamprey 1963; Watson 1966; Bell 1969; Casebeer & Koss 1970; Stewart & Stewart 1970; Jarman 1974; Owaga 1975; East 1984; Hansen *et al.* 1985; McNaughton & Georgiadis 1986; Murray 1993). That is, all herbivores to some extent select grass of a certain species, growth stage, height, and quality (Watson 1966; Gwynne & Bell 1968; Owen-Smith & Cumming 1993). They can also be highly specific in their selection and these characteristics may be attributed to subtle modifications in physiology (Casebeer & Koss 1970; Murray 1993; Murray & Illius 2000). For example, hartebeest digest fibre more efficiently than the other ruminants (Murray 1993). Consequently, their daily intake can be lower, enabling them to be more selective foragers. However, including any more detail at this stage would over-complicate the model unnecessarily. The degree of food selectivity amongst components is subsequently kept relatively basic.

The amount of green grass available, therefore, depends on the time scale in which it remains green. Braun (1973) states the decline in *CP* content of grass occurs rapidly in the first six weeks of growth (Figure 4.9). This is particularly pronounced in the long grassland samples, as long grass species yield a higher proportion of stems, the majority of which emerge in the first 8 weeks of growth (Braun 1973).

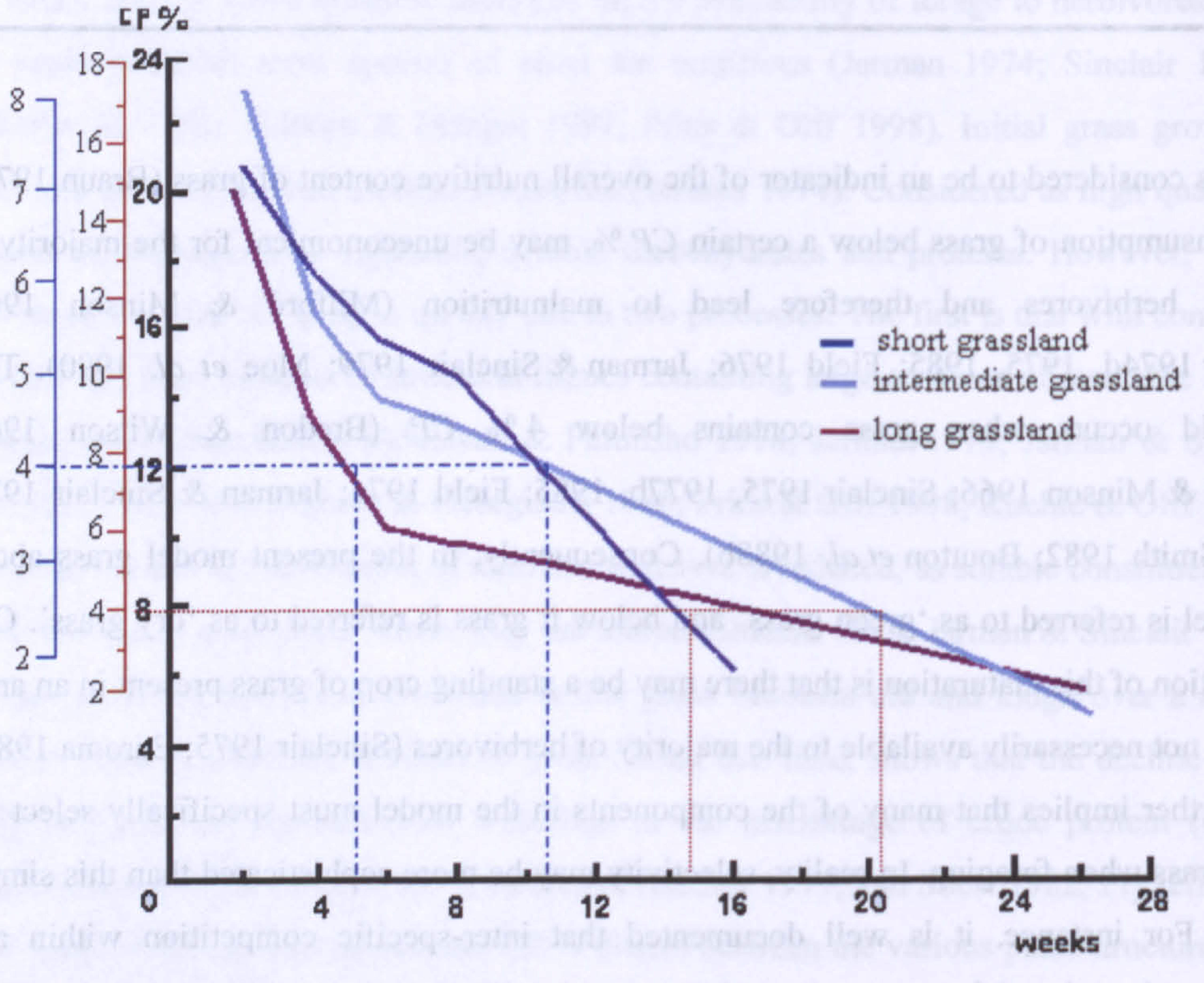

Figure 4.9 Crude protein percentage with time when the grass grows undisturbed (Braun 1973). The red and blue dotted lines indicate Sinclair (1985) *CP %* range aligned to Braun's (1973) data and Duncan's (1975) *CP %* range, respectively.

However, figure 4.9 shows that even after 16 weeks, grass has not declined below a *CP* content of 6 %. Braun (1973) confirms this in his study, which states that the *CP* % of standing crop remained above 5 %, even in the dry season. In contrast, Sinclair (1985) found *CP* values ranging from 8 to 2 %, Duncan (1975) quotes a range from 17.1 to 2.8 % (see Table 4.8; Jarman & Sinclair 1979) and Dougall (1963) identified a range of 35 to 3 % in grasses in the Mara Reserve in Kenya. Moreover, after further investigation Dougall (1964) observed that the crude protein content of *Themeda triandra*, the major grass species in the Mara, was 6.57 to 7.28 % for green grass, 3.06 to 3.72 % for bulking grass and 2.45 to 2.82 % for senescent grass. He also illustrated the time scale in which these stages were reached (Figure 4.10).

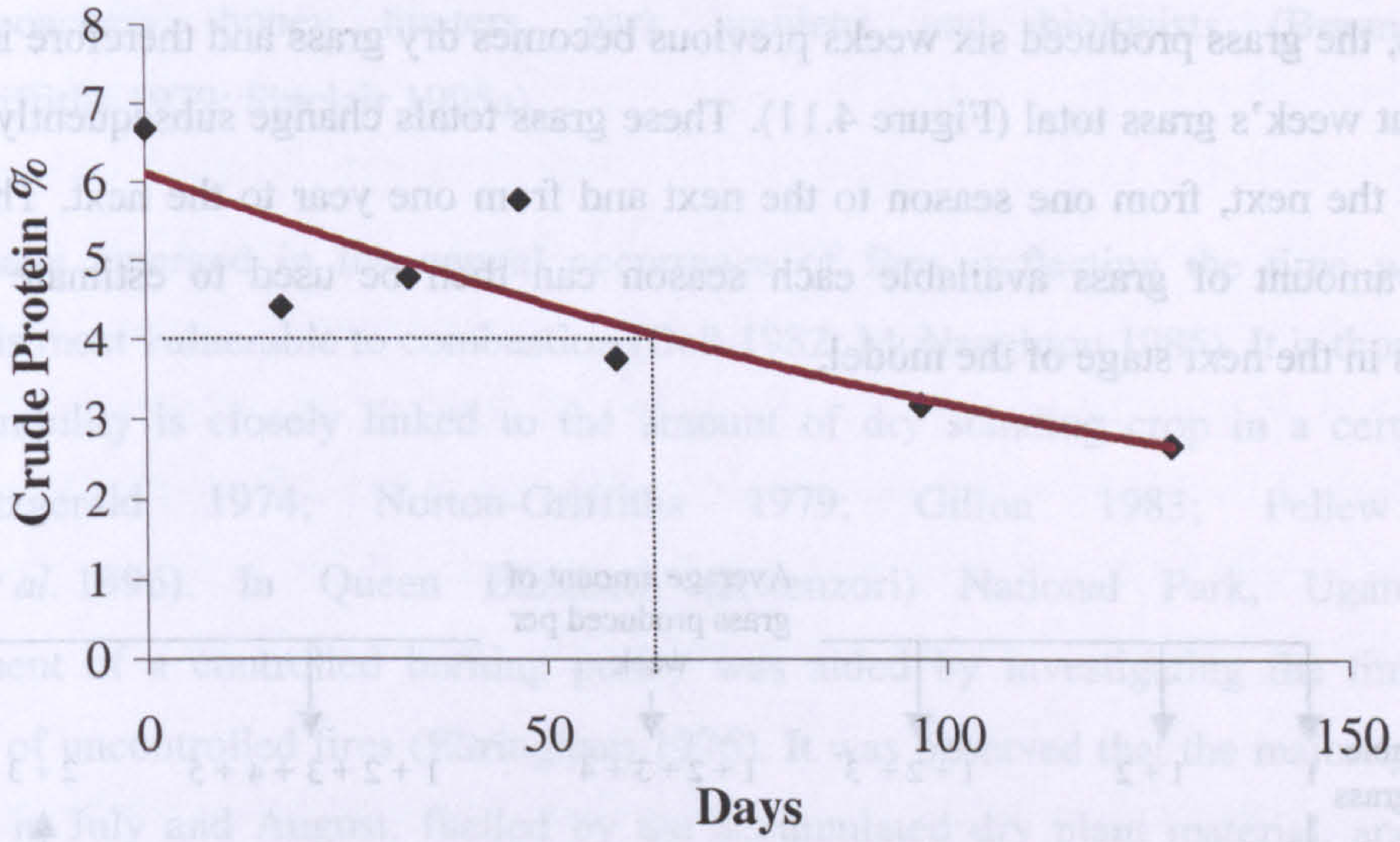

Figure 4.10 Crude protein percentage of *Themeda triandra* at advancing stages of maturity (Dougall 1964). Dotted line indicates the time taken to reach a 4 % *CP* level.

According to the data in figure 4.10, *Themeda triandra* becomes dry grass after approximately 60 days, or 8 weeks, from its initial growth. Furthermore, if it is assumed that Braun's (1973) data appropriately depicts the decline in *CP* content of grass, then Duncan's (1975) and Sinclair's (1985) ranges can be superficially applied to figure 4.9. The ranges are aligned by assuming the maximum *CP* %, given by both authors, represents the *CP* content of grass in its first week of growth and the minimum *CP* % represents the lowest *CP* level reached. This crudely reveals that grass reaches its 4 % *CP* level between 14 and 20 weeks using Duncan's range and 5 to 10 weeks using Sinclair's. Unfortunately, this exercise only demonstrates that there is absolutely no similarity between sources and there is no further information to confirm the accuracy of any one of these. Consequently, green grass can become dry grass at any point from 5 weeks onwards. Of course, at this early stage in the model it is impossible to determine whether the length of time prior to maturation significantly effects the amount of green grass available to herbivores and subsequently their population numbers. These effects will therefore be analysed in chapter 8, once herbivore components have been established in the model.

As maturation is based on a weekly time-scale, it can be incorporated into the model by dividing each module into the appropriate number of weeks it contains. For instance, the dry season modules are divided between 22 weeks and the wet season modules by 30 weeks. As each week passes, the weekly amount of grass grown (appropriate to the season) can be added to the amount of green grass still available from the previous week, while the green grass that becomes dry grass is removed. For example, if green grass maturation occurs after 6 weeks, the grass produced six weeks previous becomes dry grass and therefore is removed from that week's grass total (Figure 4.11). These grass totals change subsequently from one week to the next, from one season to the next and from one year to the next. The average weekly amount of grass available each season can then be used to estimate herbivore numbers in the next stage of the model.

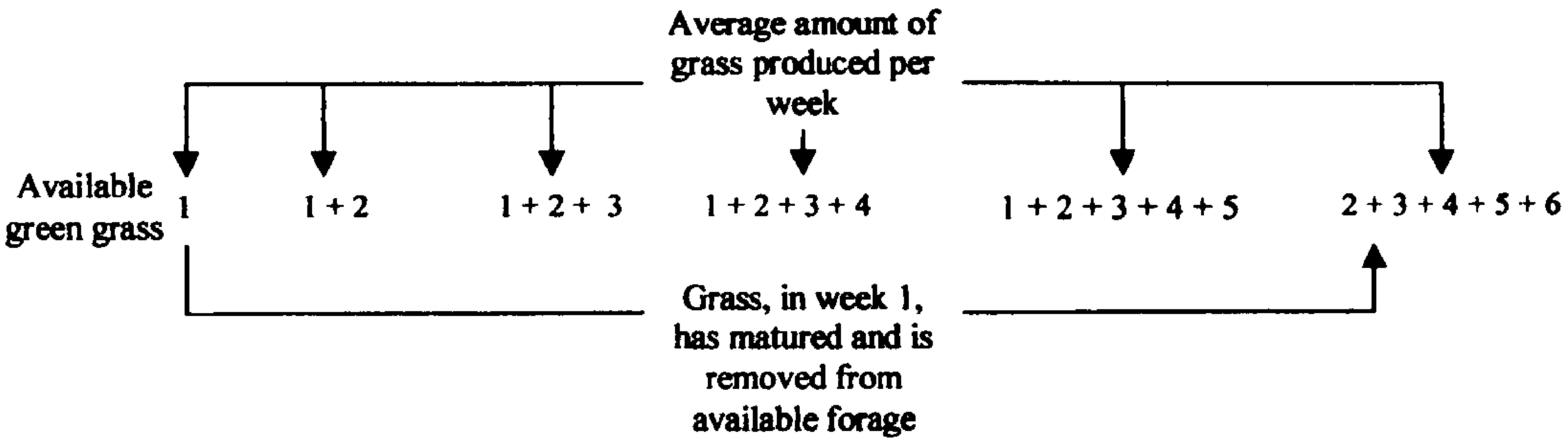

Figure 4.11 Illustration of weekly green grass availability.

Of course, the amount of dry grass removed depends on the amount of grass remaining after fire and herbivory have taken place. The effects of large herbivore grazing will be discussed further in section 5.5.2 & 6.3, but the following sections take into account these other removal agents.

4.4.2 The impact of fire

As previously suggested, fire also influences the amount of grass available (Norton-Griffiths 1979; Bell 1982; McNaughton 1983; Sinclair 1985; Gichohi *et al.* 1996). The Serengeti-Mara ecosystem has for decades been largely maintained by periodic fires (Norton-Griffiths 1979; Sinclair 1985). Some are caused naturally by lightning, chemical action or friction, but since man started to use fire as a tool, fires have increased in frequency and regularity, and contributed to the alteration of the local vegetation (Buechner & Dawkins 1961; de Vos 1969; Gillon 1983; Moe *et al.* 1990; Gichohi *et al.* 1996). Many of these fires are started either by the surrounding cultivators, who burn their rangelands annually, which then sweep uncontrolled into the park (Buechner & Dawkins 1961), or by the Massai to encourage grazing for their cattle and to discourage the tsetse fly and ticks (Talbot & Talbot 1963). Further contributors are cattle raiders, poachers, honey hunters, park wardens and biologists (Braun 1973; Norton-Griffiths 1979; Sinclair 1995a).

Patterns have emerged in the annual occurrence of fires, reflecting the time when the grassland is most vulnerable to combustion (Bell 1982; McNaughton 1985). It is thought that this vulnerability is closely linked to the amount of dry standing crop in a certain area (Vesey-Fitzgerald 1974; Norton-Griffiths 1979; Gillon 1983; Pellew 1983; Gichohi *et al.* 1996). In Queen Elizabeth (Rwenzori) National Park, Uganda, the establishment of a controlled burning policy was aided by investigating the timing and frequency of uncontrolled fires (Eltringham 1976). It was observed that the majority of fires broke out in July and August, fuelled by the accumulated dry plant material, and spread widely throughout the area consuming most vegetation in its wake (Eltringham 1976; Edroma 1984). It is not unreasonable to assume that the Serengeti has a similar burning regime to Queen Elizabeth National Park. The area is particularly vulnerable to fires in July, as it is the driest month of the year with a potentially large standing crop left over from the wet season. As the dry season proceeds, the amount of dry material is able to build-up until there is enough fuel for another conflagration to occur (Gichohi *et al.* 1996).

More detailed investigations within the Serengeti have revealed that the frequency of fires not only varies between the three zones, but also annually (Daubenmire 1968; de Vos 1969). One such study by de Vos (1969) led to him concluding that fire did not occur at the same frequency in all vegetation types. Sinclair (1975) investigated this further by mapping the variations in frequency of fire across the Serengeti on a systematic basis from 1963 to 1972 (Figure 4.12). Norton-Griffiths (1979) concluded from these surveys that fires occurred at a higher frequency in the woodlands compared with the plains, undoubtedly due to a larger proportion of combustible structural material in the long grass species growing in the northern half of Serengeti. Furthermore, it is thought that the absence of people in the south-east is a contributory factor to the low incidence of fire on the plains (Eltringham 1976).

Sinclair (1975) suggests the average area burnt each year is 62 % in the woodlands and 19 % on the plains. Norton-Griffiths (1979) goes on to reveal that the frequency of burning has decreased considerably from 1962 to 1974 (Figure 4.13). Further investigations carried out by Dublin *et al.* (1990) confirmed this decrease, particularly in the northern Serengeti. They compared Sinclair's (1975) figures for 1960, when fires were frequent and severe, with Dublin's (1986) observation that the area burnt was only 5 % for the 1980s. It was concluded that the reduction in incidence of fire was due to a combination of factors. These included the removal of potential grass fuel by the increased numbers of wildebeest, following the elimination of rinderpest and the prohibition of human-induced fires (Dublin *et al.* 1990; Murray *et al.* 1992; Gichohi *et al.* 1996). In fact, an estimated 2 % of the area consumed by fires during the 1980s were attributed to natural causes (Moe *et al.* 1990).

These fire percentages can be manipulated to give an estimated annual percentage burn, or more aptly, the dry season percentage burn. Moreover, as two separate bouts of fire occur during this season, one more intense than the other, a portion of this percentage burn is allocated to each. For this, it is simply assumed that two-thirds of the total incidence of fire occurred in July, when the amount of dry grass is at its greatest following the wet season, and the remainder in August (Gichohi *et al.* 1996). From figure 4.13, burning figures in the north are considered to represent zone 1, the centre of the park represents zone 2 and the plains represent zone 3. Taking the data points from Norton-Griffiths' graphs, and extending the trend back to 1960 and forward into the 1980s (using Dublin's (1986) burning values for this decade as the minimum), annual burning percentages for each module was established (Appendix table 1).

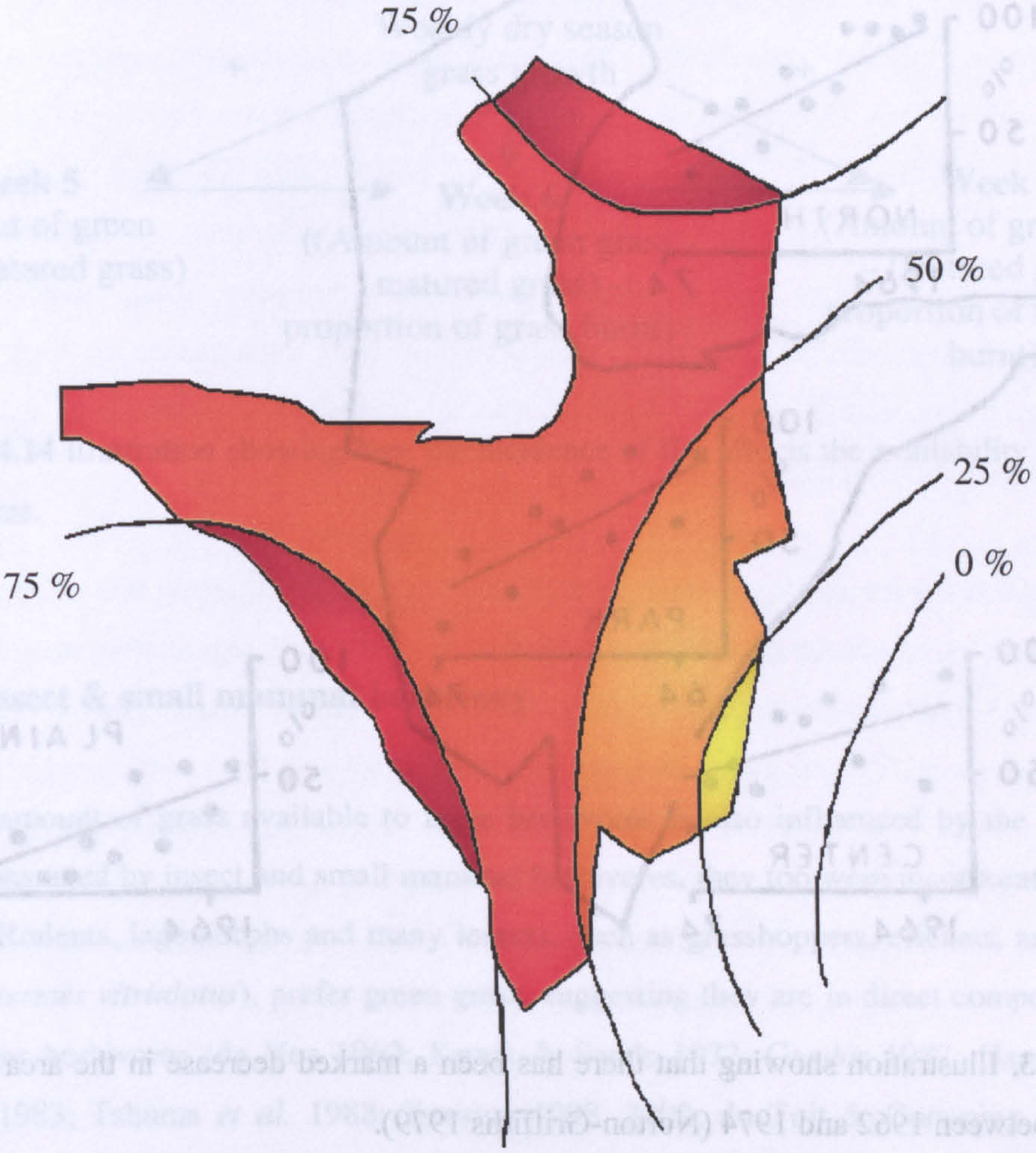

Figure 4.12 The frequency of burning in different areas of the park between 1963 to 1972 (Sinclair 1975; Norton-Griffiths 1979).

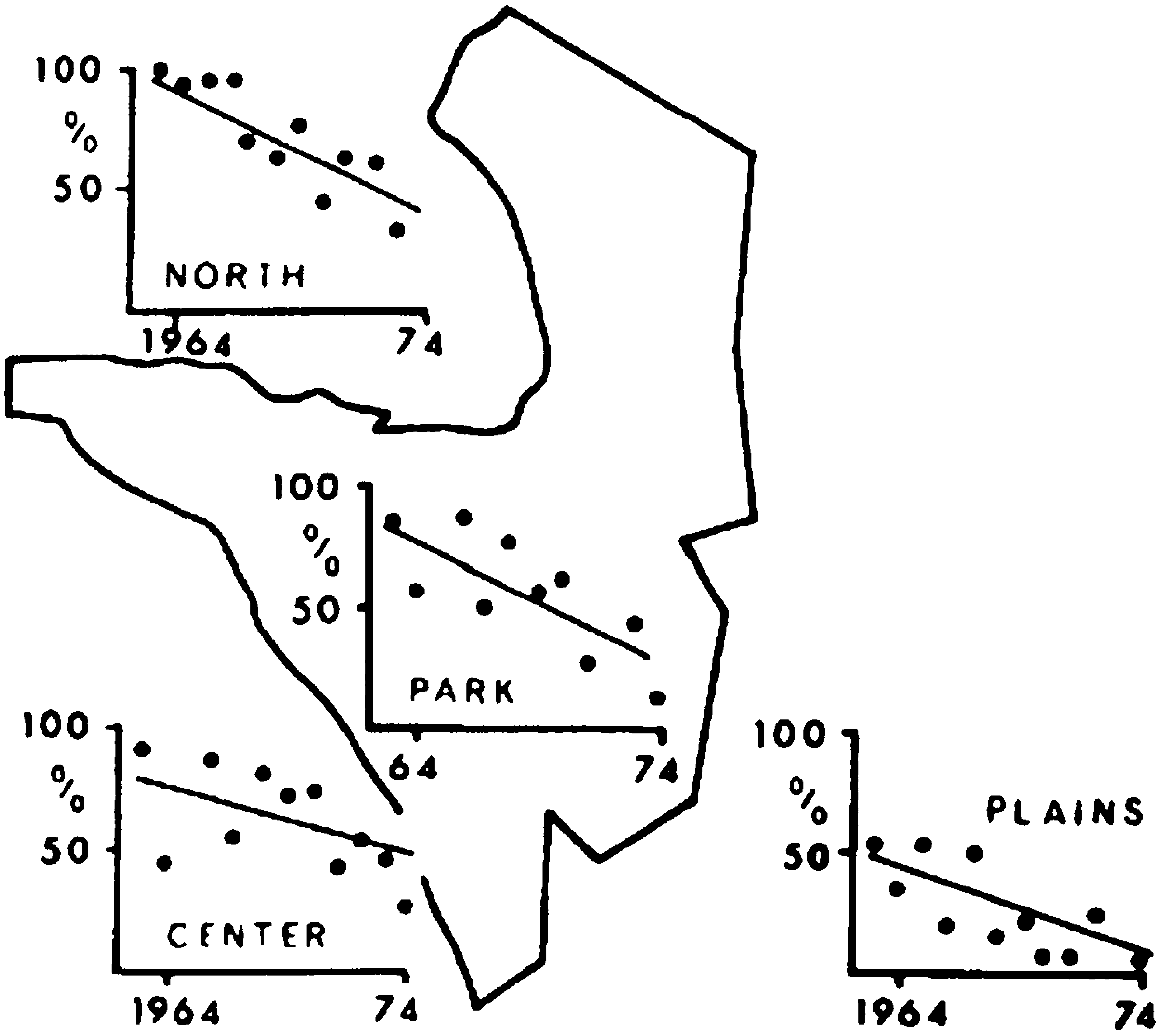

Figure 4.13, Illustration showing that there has been a marked decrease in the area burned each year between 1962 and 1974 (Norton-Griffiths 1979).

To incorporate annual fire into the present model, it was first assumed that fires occurred at the beginning of the 6th week (mid-July) and 13th week (mid-August) of every dry season. The appropriate proportion of grass burnt during these fires, for a particular zone and year, can then be removed from the amount of green grass available following the removal of matured grass that week. Furthermore, the weekly maturation take-off following the occurrence of fire, reflects the amount of grass left to mature (Figure 4.14). By burning a proportion of the total amount of grass available, the actual amount of grass burnt will vary. Consequently, when herbivory is incorporated into the model (see section 4.4.3 & 5.5.2), fires will appear to be suppressed by higher levels of grazing, as they are in the wild (Gichohi *et al.* 1996).

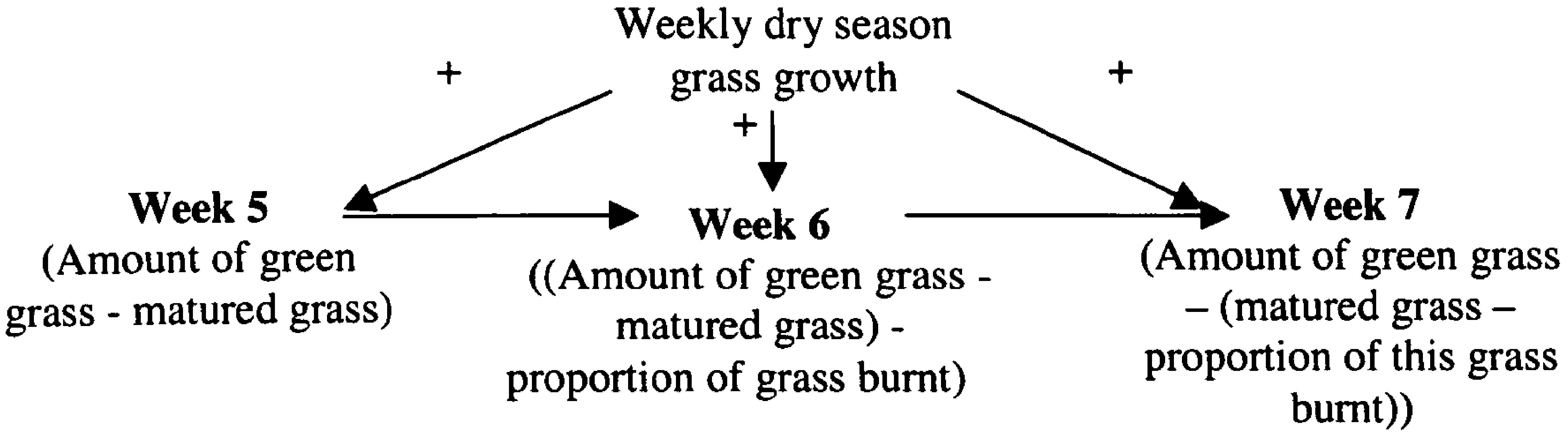

Figure 4.14 Illustration showing how the incidence of fire affects the availability of grass to herbivores.

4.4.3 Insect & small mammal herbivory

As the amount of grass available to large herbivores is also influenced by the amount of grass consumed by insect and small mammal herbivores, they too were incorporated into the model. Rodents, lagomorphs and many insects, such as grasshoppers, crickets, and termites (*Macrotermes vitrialatus*), prefer green grass, suggesting they are in direct competition with the larger herbivores (de Vos 1969; Kruuk & Sands 1972; Gander 1982; Happold 1983; Josens 1983; Tshuma *et al.* 1988; Keesing 1998, 2002; du Toit & Cumming 1999). For example, the insects of the superfamily Acridoidea make up a large proportion of the order Orthoptera (grasshoppers and crickets), which have become renowned for their efficient style of herbivory and the significant impact on the grasslands they frequent (du Toit & Cumming 1999). The Serengeti-Mara ecosystem is no exception, with Sinclair (1975) suggesting that grasshoppers remove a considerable amount of grass. In addition, both de Vos (1969) and Keesing (2002) have observed that rodents and lagomorphs directly compete with ungulates, particularly at high population densities when they can consume considerable quantities of green grass. However, observations made by Deshmukh (1986) in Nairobi National Park revealed that rodent and insect populations were low and unlikely to remove significant primary production. Controversially, Deshmukh suggests this is the case in many other African savannahs. Despite this conflicting information, the inclusion of small mammal and insect herbivory into the present model was considered to be appropriate.

Fortunately, the information required to do this is provided by Sinclair (1975). He investigated the 3 main herbivore groups, large ungulates, small mammals and insects. From sample plots in the grasslands, he found that grasshopper species, such as *Mesopsis abbreviatus*, *Coryphosima stenoptera*, *Afrohippus taylori*, *Dnopherula backlundi*, *Acrotylus elgonensis* and *A. patrualis*, were so much more abundant than all other invertebrate herbivores put together, that the latter could effectively be ignored. Having gained this information, he estimated grasshopper biomass using mark-recapture experiments during different seasons and measured their food consumption via feeding trials. He was then able to calculate the food off-take of grasshopper populations in different grassland types for each month.

When investigating the small mammal populations, Sinclair (1975) found that although some thirty-six species of rodent have been recorded in the Serengeti region (Swynnerton 1958; Misonne & Verschuren 1966; Laurie 1971) only five were dominant, *Otomys tropicalis*, *Praomys natalensis*, *Lemniscomys striatus*, *Mus minutoides* and *Arvicanthis niloticus* and of these, the latter, contributes to 86 % of the total rodent population (Happold 1983). Sinclair (1975) went on to obtain the biomass of rodents in the long grasslands and around kopjes from live trapping and measured consumption rates. He then did the same for other small mammals, such as spring hares (*Pedetes caffer*) and hyrax.

The results of these two investigations are given in tables 4.9 & 4.10. Sinclair (1975) concluded that grasshopper populations frequently dropped during the dry season following a reduction of habitat from burning and grazing by ungulates, the cessation of breeding, and the disappearance of adults through diapause or mortality (Robertson & Chapman 1963; Phipps 1968). Consequently the invertebrates contributed very little to the total off-take at this time. During the wet season their numbers increased, and their impact on the grass layer was at least equal to, if not greater than that of the resident ungulates (Sinclair 1975). Small mammals, on the other hand, remained in low numbers throughout the year (Sinclair 1975). Keesing (1998, 2002) suggests that small mammal populations are, in fact, limited by the foraging of ungulates, and their constant low numbers are simply a reflection of the large number of ungulates present in the Serengeti (de Vos 1969).

The impact of this herbivory on overall grass availability was incorporated into each module by deducting the proportion of green grass eaten by small mammal and invertebrate populations, calculated from Sinclair's (1975) data given in tables 4.9 and 4.10.

Table 4.9 Proportion of green grass required by invertebrate and small mammal populations each season in zone 1 and 2 estimated by dividing the amount of grass eaten by the total amount of grass available measured by Sinclair (1975).

Month	Monthly green grass requirements (kg/ha)		Total amount of grass available
	Invertebrates	Small mammals	
November	34.9	3.3	589.8
December	56.5	8.9	1277.8
January	56.5	8.9	1907.8
February	56.5	8.9	2486.8
March	56.5	8.9	3286.9
April	56.5	5.0	4384.0
May	56.5	5.0	5036.9
Total wet season requirements\available (kg/ha)	373.9	48.9	18,970
Proportion of green grass eaten in the wet season	0.02	0.003	
June	56.5	5.0	5137.6
July	10.5	5.0	0
August	5.9	3.3	0
September	4.6	3.3	0
October	4.6	3.3	0
Total dry season requirement\available (kg/ha)	81.6	19.9	5137.6
Proportion of green grass eaten in the dry season	0.02	0.004	

Table 4.10 Proportion of green grass required by invertebrate and small mammal populations each season in zone 3 estimated by dividing the mean monthly amount of grass eaten by the total amount of grass available measured by Sinclair (1975).

Month	Monthly green grass requirements (kg/ha)		Total amount of grass available
	Invertebrates	Small mammals	
November	17.9	17.91.8	404.4
December	41.8	41.84.6	957.6
January	41.8	41.84.6	1422.9
February	41.8	4.6	1905.8
March	41.8	4.6	2379.1
April	41.8	2.6	3356.9
May	41.8	2.6	3850.3
Total wet season requirement\available (kg/ha)		25.4	14,277
Proportion of green grass eaten in the wet season	0.02	0.002	
June	41.8	2.63	5328.0
July	5.5	2.63	0
August	3.3	1.82	38.4
September	2.8	1.82	92.9
October	2.8	1.82	154.9
Total dry season requirement\available (kg/ha)	56.2	10.7	5614.2
Proportion of green grass eaten in the dry season	0.01	0.002	

4.5 DRY GRASS

As previously discussed in section 4.2.1 the quality of grass decreases over time until green grass becomes dry grass. As grass continues to mature on a weekly basis, the amount of dry grass present accumulates. Furthermore, the rate of accumulation is far greater than the rate of grass decomposition. Deshmukh (1985) reports that even after 2 years, 40 % of the initial dry grass still remains. This is comparable to studies carried out by Christine (1979) in Australian semi-arid grasslands and Koelling & Kucera (1965) in natural grasslands in the USA. Deshmukh (1986) further noted that in Nairobi National Park, slow decomposition led to a high proportion of dead and dying standing crop compared to live grass (Figure 4.15). This implies that unless this low quality, dying and dead grass is removed, the grasslands in the Serengeti-Mara ecosystem could potentially consist largely of dry grass.

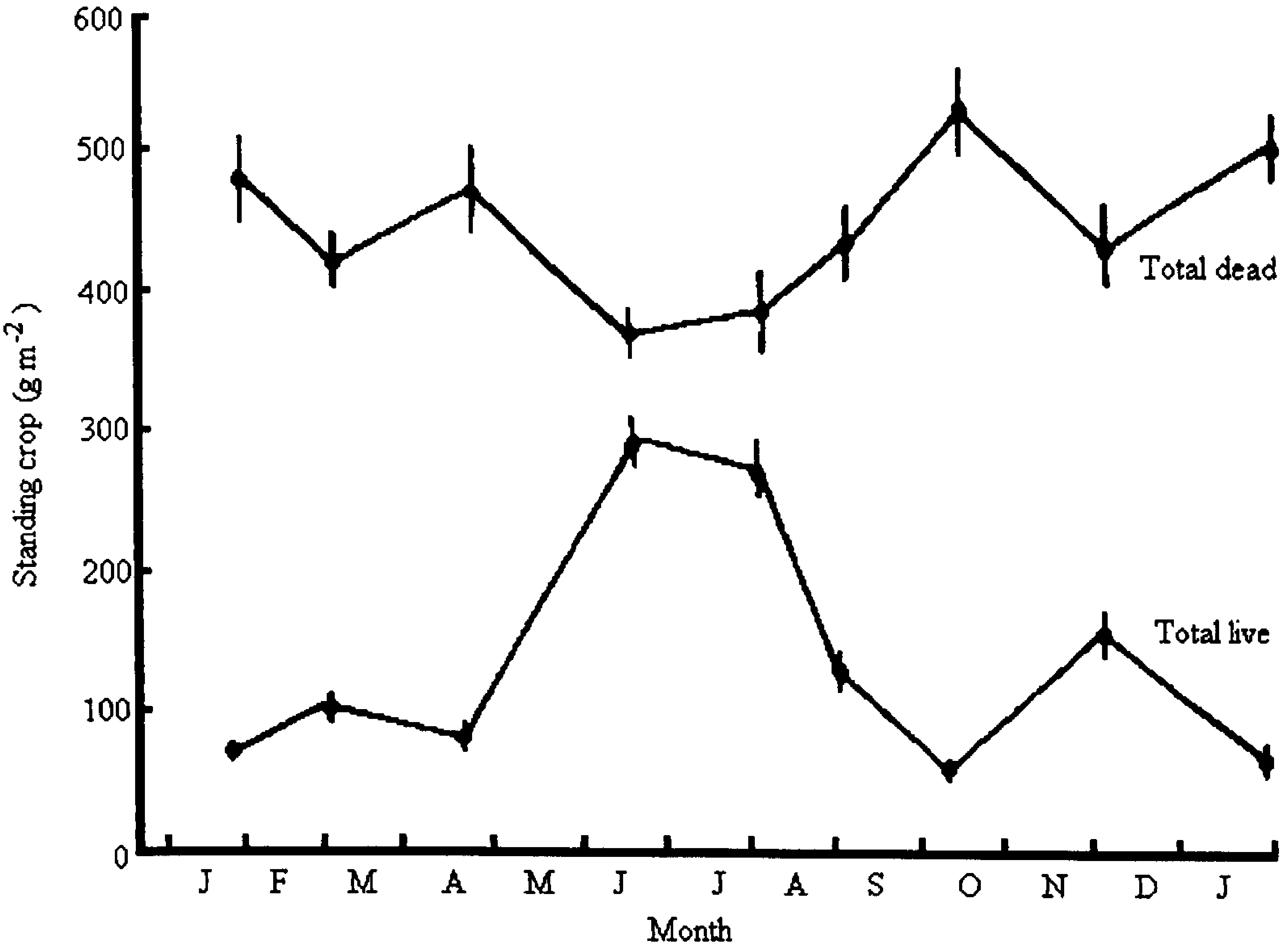

Figure 4.15 Monthly changes in biomass of living grasses and dead standing crop in Nairobi National Park. Vertical bars are standard error of means (Deshmukh 1986).

Nevertheless, this increasing build-up of dry grass is considered to be important to a number of components within the ecosystem. It may not be of high quality, but it is still a valuable resource, if it can be utilised. Non-ruminants, such as zebra, have this ability and readily eat dry grass (Owaga 1975; Owen-Smith & Cumming 1993). Subsequently, in times when green grass is scarce, zebra may have an advantage over similar sized ruminants (Duncan 1992; Hack *et al.* 2002; Saltz 2002). As a consequence, the annual abundance of dry grass is incorporated into the modules. In addition to large herbivore grazing, which will be discussed later in section 5.5.2 & section 6.3, the amount of dry grass within each module is subject to two further factors, fire and termites.

4.5.1 Fires

Deshmukh (1985) states that unless dry grass is burned, decomposition and nutrient cycling are very slow. Of course, it has already been suggested, in section 4.2.2, that the incidence and intensity of fire and the amount of dry material present are strongly correlated (Daubenmire 1968; Gillon 1983; Pellew 1983; de Vos 1969). However, predicting this relationship to incorporate it into the model has already been achieved, as the fires that affect green grass availability, obviously affect dry grass as well (Bell 1982). The same annual proportions of 'grass burnt' can therefore be deducted from dry grass figures (see section 4.4.2; Appendix table 1). Of course, fire reduces the amount of dry grass in two ways, by burning it directly and by burning green grass before it can become dry grass.

4.5.2 Termites

Termites also remove a considerable proportion of dry grass in the Serengeti-Mara ecosystem (Glover *et al.* 1964; Bourlière & Hadley 1970; Josens 1983). Herbivory by isoptera is included in the modules because, like grasshoppers, they are renown for their impact on the ecosystems they inhabit (de Vos 1969; Bourlière & Hadley 1970; Ohiagu & Wood 1979; Morris *et al.* 1982; Josens 1983). Within these colonies, workers forage very thoroughly by radiating into the surrounding area collecting dry, dead, or decomposed grass (Josens 1983). It has been suggested that termites can strip up to 10 % of vegetation from the land surface (de Vos 1969). Furthermore, inter-invertebrate competition is virtually non-existent, as they are the principle invertebrates capable of digesting lignocellulose (Josens 1983; Myles 1996).

In the Serengeti, there are a number of different species of termite, including four *Trinervitermes* spp., two *Odontotermes* spp., *Macrotermes vitrialatus* and *Hodotermes mossambicus* (Kruuk & Sands 1972). However, there are difficulties in of sampling their natural populations, particularly those species that are entirely subterranean, such as *Odontotermes* spp. and *Hodotermes mossambicus* (Josens 1983). Furthermore, feeding rates and biomass figures for termites have not yet been investigated for the Serengeti. Fortunately, an extensive investigation by Josens (1983) on the trophic impact of termite consumers, revealed that this impact is relatively constant. In dry savannahs with approximately 400 mm of annual rainfall, such as the northern Serengeti, termites consume 31 % of the dry matter in the area (Josens 1983). This figure is, therefore, used in the each module to represent the amount of dry grass consumed by termites each week. Interestingly, Sinclair (1975) reports that termites do not frequent the plains. However, his observations were based on the presence of termite mounds. Subterranean termite species, that do not build mounds may still be present. For the purposes of the model, this was assumed to be the case and the influence of termites was included in all the modules.

4.6 OVERALL AVAILABILITY OF GRASS

In summary, by combining all the influencing factors, rainfall, grass maturation, fire, insect and small mammal herbivory, the amount of green grass available to large herbivores can be estimated for the six modules. Furthermore, the amount of dry grass accumulated each week, due to green grass maturation, can also be assessed. The weekly availability of this dry grass to some of the large herbivores within each module, can then be established by incorporating the effects of fire and termites. The average weekly amount of green grass and dry grass available for each module can then be used to calculate herbivore numbers as addressed in the following chapters.

CHAPTER 5: HERBIVORE SURVIVAL AND RECRUITMENT

5.1 INTRODUCTION

In the last chapter, the amount of green grass available to herbivores was estimated. Following on from this, the amount of food allocated to each individual within a population, can be calculated. This chapter examines this allocation and the subsequent consequences for the survival and recruitment rates of the herbivore components included in the model (see section 2.3.1). In order to do this, a set of inter-linking Excel tables were constructed, working through the allocation of food resources and the resulting survival for each herbivore component. The mechanics of these tables are described below, using the migratory wildebeest population as an example. The survival and competitive influences of other grazers are then discussed in chapter 6.

5.2 POPULATION SIZE AND RESOURCE ALLOCATION

Resource allocation to each individual in a population is influenced by three factors. Perhaps the most obvious of these is the amount of food available to the whole population at a specific time. As discussed in previous chapters, significant variations in resource availability occur seasonally. Such seasonal variations are also seen to affect the other two factors; the number of individuals within the population and the proportion of individuals within various stages of their life history. The influences of these factors are combined in the model in order to generate a figure representing the amount of food available per individual, which can then be used to predict seasonal survival.

5.2.1 Population numbers

Within the model, population numbers are generated from season to season. This is initiated by using the population numbers for migratory wildebeest in the dry season of 1960. At this time, the Serengeti-Mara ecosystem was estimated to contain 234,000 migratory wildebeest (Grzimek & Grzimek 1960; Hilborn *et al.* 1995; Mduma *et al.* 1999). This dry season figure can be transformed into wet season numbers via the dry season survival rate. In turn, these wet season numbers can be carried forward into the next dry season via a wet season survival, and so on and so forth. As an example, the number of animals that survive the dry season in 1960 are then represented in the wet season of 1960 (Figure 5.1).

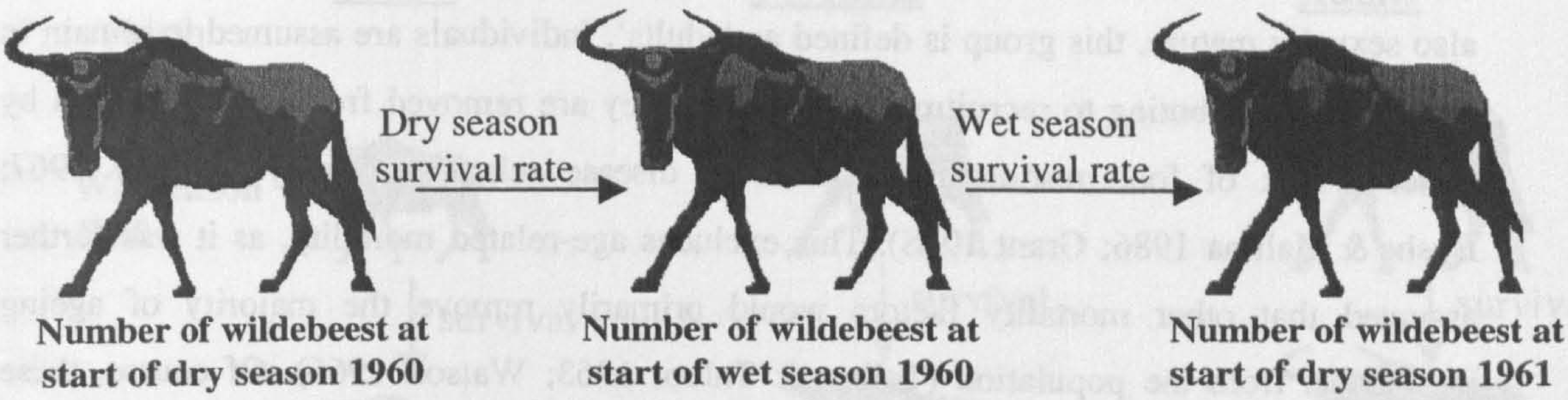

Figure 5.1 Illustration showing the regulation of the migratory wildebeest population from season to season.

The model also incorporates three significant life history stages (functional groups) seen within the wildebeest population. Differences between these groups, such as the amount of food required and the direct use of a particular resource, can have significant consequences on the survival of individuals within those stages (Blaxter 1968, 1989; Dunham & Murray 1982; Murray 1982b; Murray & Illius 2000). One of the age groups chosen to represent the life history stages of importance are 'young' individuals still dependent on their mothers' foraging capabilities (McNaughton & Georgiadis 1986). This maternal dependency stems from the fact that these young are reliant on their mother's milk. Her success at foraging has a direct consequence on the quality and quantity of milk her offspring receive, influencing their survival (Blaxter 1968, 1989; Sadlier 1969; Robbins & Robbins 1979; Clutton-Brock *et al.* 1987a). These wildebeest calves are generally nursed until the following year's calf is born at which point they are weaned. This 'young' group therefore includes individuals up to the age of one year (Talbot & Talbot 1963; Watson 1967; Delany & Happold 1979).

The second group identified is 'juveniles'. This group includes individuals that are nutritionally independent, but have not reached adult size and are not yet sexually mature. For wildebeest, although they become fertile by about 16 months, females are generally over two years old before they produce offspring, while males do not mate until four to five years of age (Talbot & Talbot 1963; Estes 1966; Watson 1969; Kingdom 1997; Delany & Happold 1979; Mduma *et al.* 1998). However, as wildebeest have a polygamous mating system, it is female fertility that has a direct influence on recruitment (Watson 1969). Juveniles, therefore, include all individuals between one and two years of age.

The final group incorporates all individuals that are not only nutritionally independent, but also sexually mature, this group is defined as 'adults'. Individuals are assumed to remain in this group contributing to recruitment rates, until they are removed from the population by either a lack of food resources, predators or disease related mortality (Murray 1967; Boshe & Malima 1986; Grant 1988). This excludes age-related mortality, as it was further assumed that other mortality factors would primarily remove the majority of ageing individuals from the population (Talbot & Talbot 1963; Watson 1966). Of course, these factors affect all the functional groups, but their influence on each can vary. For instance, hyaenas prefer to predate on young, as wildebeest within this group are particularly vulnerable (Watson 1966; Kruuk 1972; Hofer *et al.* 1993). Another example is that juveniles are particularly susceptible to the 'yearling disease', rinderpest (see section 2.3.2). By separating individuals into functional groups, the influence of pre- and post-reproductive mortality factors on recruitment and, thus, population dynamics can be determined (Green *et al.* 1994). Consequently, separate numbers of adults, juveniles and young are required. According to Mduma *et al.* 1999, the migratory wildebeest population in January 1960 consisted of 203,597 adults and 30,630 juveniles. They go on to state that by the start of the dry season in June, the number of young that had survived represented 18 % of the adult population. Assuming that the population remained unscathed from January, this constitutes 36,647 young (0.18 x 203,597). These three figures can be used to initiate the model.

Within the model these functional groups are linked so that individuals from one can enter the next as they mature. For wildebeest, young are usually born in the wet season, particularly around February and then weaned a year later (Talbot & Talbot 1963; Estes 1966, 1976, 1991; Watson 1966, 1967, 1969; Fraser 1968; Sinclair 1977a; Delany & Happold 1979; Stuart & Stuart 1997; Kingdom 1997; Mduma *et al.* 1999). The number weaned represents the number of young that become juveniles during the following wet season. Similarly, those juveniles that survive the next year are added to adult numbers during the following wet season (Figure 5.2).

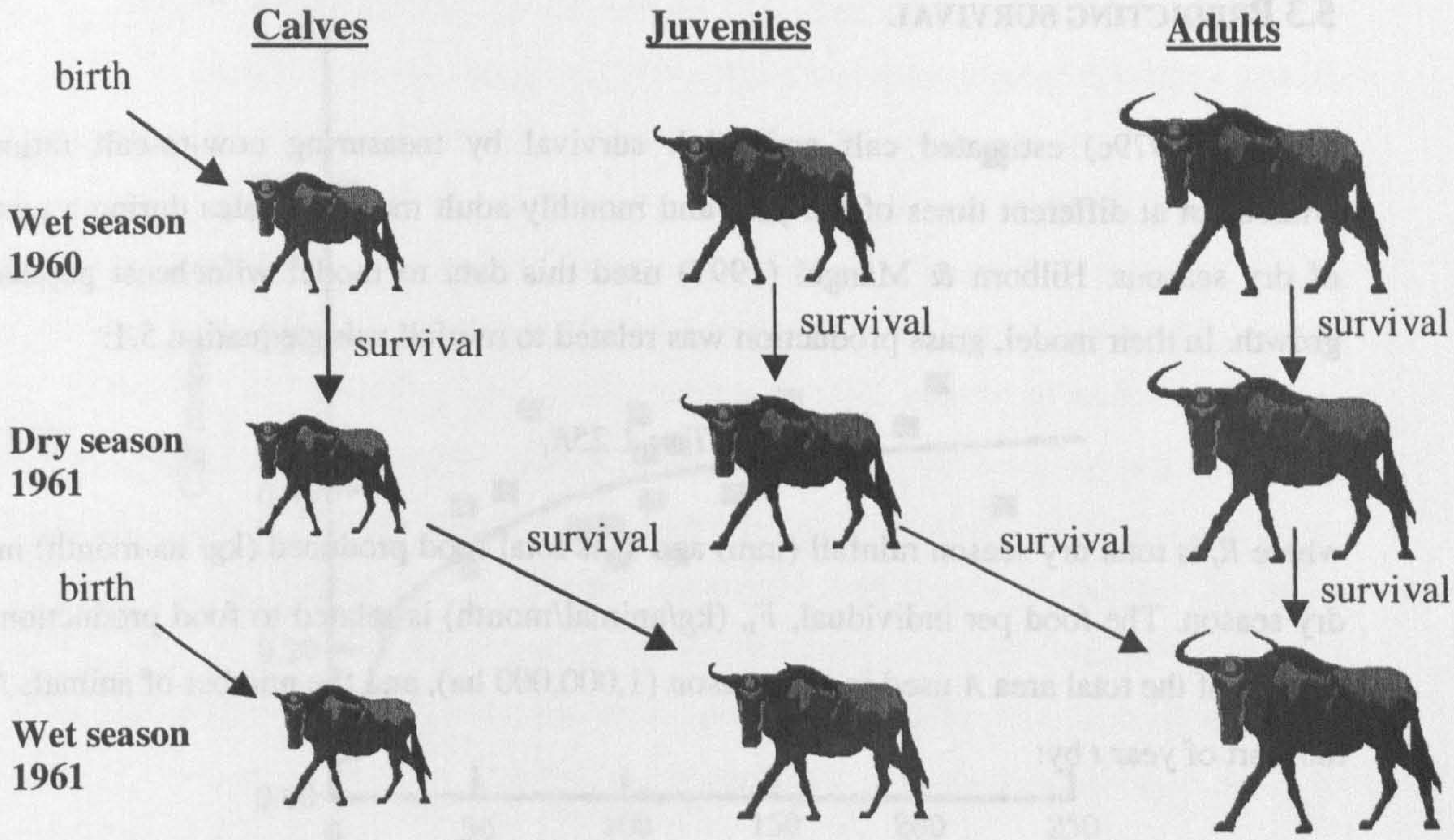

Figure 5.2 Diagram to show the stages of maturation and recruitment within a wildebeest population.

5.2.2 Resource per individual

The amount of food available to each individual wildebeest for the appropriate zone and season is calculated using the weekly grass availability values estimated in chapter 4.

Juveniles and adults are treated separately as their intake rates and feeding capabilities vary. These differences in diet are characterised by differences in weight, and can be dealt with by using biomass equivalents. Therefore, by converting juvenile numbers into equivalent adult numbers and combining it with actual adult numbers, the average amount of resource available per 'adult' wildebeest can be calculated. The conversion figure for this is found by comparing the average juvenile (158.5 kg) with the average adult (221 kg). A similar calculation estimates the amount of food available per 'juvenile' wildebeest.

5.3 PREDICTING SURVIVAL

Sinclair (1979c) estimated calf and adult survival by measuring cow-to-calf ratios of wildebeest at different times of the year and monthly adult mortality rates during a number of dry seasons. Hilborn & Mangel (1997) used this data to model wildebeest population growth. In their model, grass production was related to rainfall using equation 5.1:

$$T_t = 1.25R_t \qquad (5.1)$$

where R_t is total dry season rainfall (mm) and T_t is total food produced (kg/ ha·month) in the dry season. The food per individual, F_t, (kg/animal/month) is related to food production per hectare of the total area A used in this season (1,000,000 ha), and the number of animals N_t at the start of year t by:

$$F_t = \frac{T_t A}{N_t} \qquad (5.2)$$

This is a very similar method to that used in the present model (see chapter 4). Hilborn & Mangel go on to determine the survival of calves, s_{calf}, t, from births in year t to their first birthday. To do this they assumed that the relationship between calf survival and the amount of food available would take the form of a Holling type-II functional response (given by equation 5.3; Holling 1959), in which the amount of food ingested is a saturating function of the amount of food available.

$$s_{calf,t} = \frac{aF_t}{b+F_t} \qquad (5.3)$$

Here the parameters a and b are constants that determine how calf survival is related to a quantity of food. $a \leq 1$ is the maximum value of calf survival and b is the value of food per individual at which survival is 50% of a. Mduma *et al.* (1999), go on to demonstrate, using Sinclair's calf survival data and their own data (collected from monthly samples of observed and estimated ratios of calves per female from July 1992 to December 1994) that this type of model reasonably fits the data (Figure 5.3). Both Hilborn & Mangel (1997) and Mduma *et al.* (1999) use a similar functional form for the relationship between adult survival and food availability.

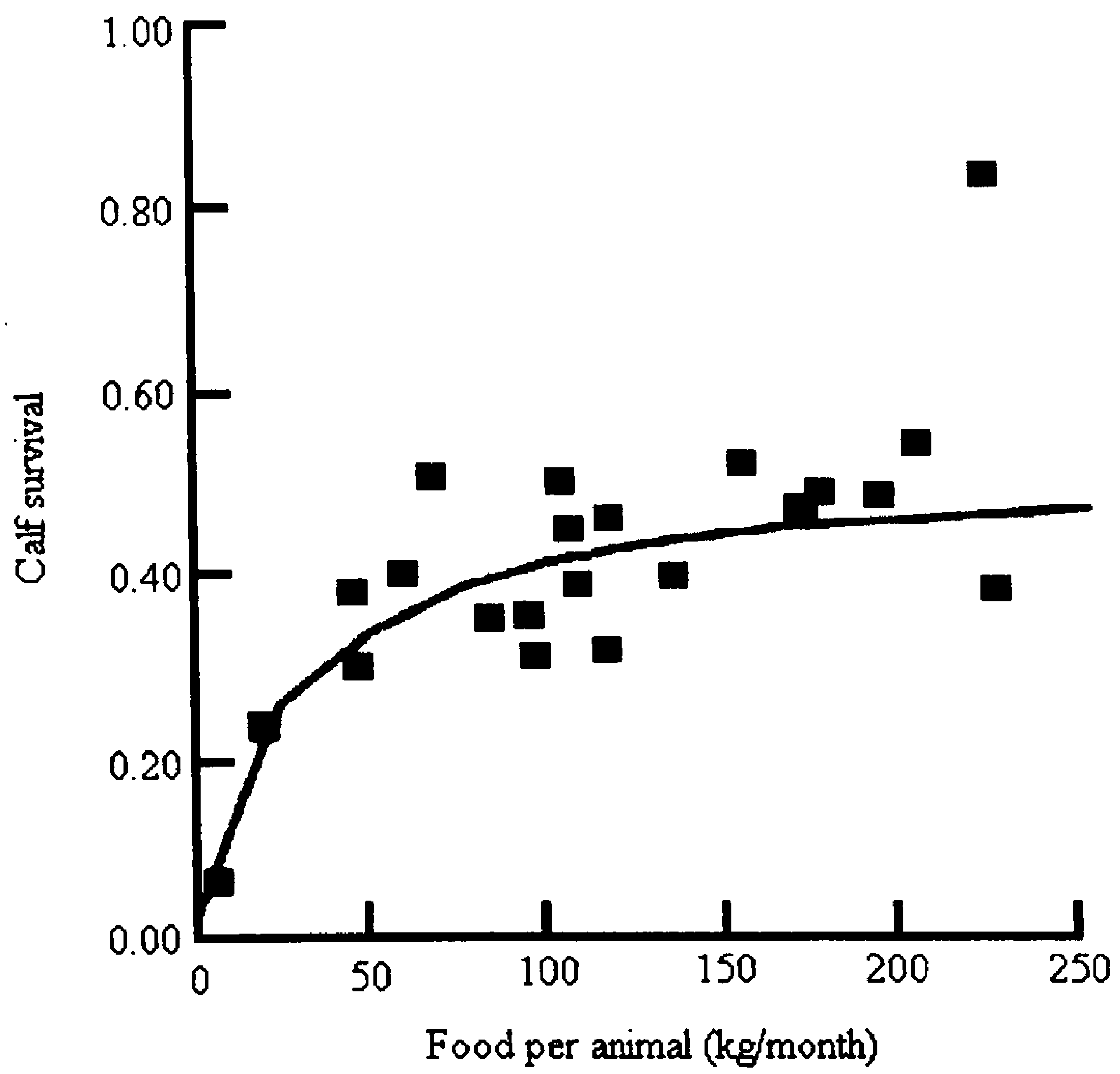

Figure 5.3 The relationship between calf survival and food per animal. The solid line is the best-fit Holling type-II functional response (Hilborn & Mangel 1997; Mduma *et al.* 1999) for the calf survival data points given by Sinclair (1979c).

As figure 5.3 indicates, one feature of this model is that the upper asymptote or maximum calf survival value is 0.4. Of course, if this model applied only to food-related mortality, the curve would be asymptotic at 1.0, when food was no longer a limiting factor. This implies that other mortality factors are limiting calf survival. Moreover, the model specifically describes the survival of wildebeest calves within an ecosystem matrix, where the influence of individual species is indistinguishable. In the present model, the aim is to successively add each component and the various mortality factors affecting them, so that changes in density at each addition can be monitored and interaction effects can be explicitly observed. As Hilborn & Mangel's model does not facilitate this, survival rates used in the model are instead based on the nutritional importance of food through the bioenergetics of each component species. This involves looking at metabolic rates, defined as the total amount of energy required from food, just to stay alive (Peters 1983; Campbell 1996). In fact, every species has a range of metabolic rates, from minimal rates, which support the basal physiological functions, such as respiration, to maximum rates, which occur during peak activity, such as running (Green *et al.* 1994).

By comparing metabolic rates as indicators of food requirements, with resource availability during a particular season, survival rates can be predicted (de Vos 1969; McNab 1980). This assumes that if 'food per animal' (F_pA) does not provide the necessary energy needed to sustain an individual, it dies (Peters 1983; Sutherland & Dolman 1994; Goss-Custard *et al.* 1995a, b). However, no animal can fuel expenditure simply from current income. There will always be times when it is unable to feed adequately and relies on stored reserves (Dunham & Murray 1982; Mangel & Clark 1988). Sinclair (1975) states the use of reserves causes a time lag in a population's response, through mortality, to a reduction in resources. Of course, the time-scale and magnitude of requirements can vary markedly, from overnight survival, to surviving a season or completing a migration (Cuthill & Houston 1997). In the present model, taking *FpA* as a weekly average per season, smoothes the daily and weekly fluctuations in resource availability. The additional influence of stored reserves on survival is, therefore, not essential.

5.3.1 Calculating metabolic rates

In order to calculate survival rates for each component in the model, metabolic rates applicable to each are required. However, since information on metabolic rates is unavailable for most of these species, a method to estimate such species-specific rates is necessary.

Campbell (1996) stated that one of animal biology's most intriguing relationships is that existing between body size and metabolic rate. By monitoring the metabolic rates of hundreds of species of birds and mammals, physiologists have determined that the amount of energy it takes to maintain each gram of body weight is inversely related to body size (Bell 1969; McNab 1980; Blueweiss *et al.* 1978; Demment & van Soest 1985; Campbell 1996). Each gram of a mouse, for instance, consumes approximately ten times more calories than a gram of an elephant. This is due to the demands of a proportionately greater rate of oxygen delivery to the body tissues in a smaller animal (Campbell 1996).

Hayssen & Lacy (1985) describe the relationship between basal metabolic rate (BMR) and body mass for various taxa of mammals, using a log linear equation:

$$\log_{10}(\text{BMR, ml O}_2/\text{g-hr}) = \mathbf{a} + \mathbf{b}\ \text{log10 (mass, g)} \tag{5.4}$$

where BMR is defined as the rate at which energy must be released metabolically in order to maintain an animal during complete rest or sleep (Silver *et al.*1969; Blaxter 1989). The results of Hayssen & Lacy's (1985) investigation are shown in appendix table 2.

Using equation 5.4, metabolic rate (BMR) can be calculated for each species in the model. For example, wildebeest are estimated to have a BMR value of 0.22 ml O_2/g-hr, using the coefficients for the intercept (*a*) and slope (*b*) for the Order Artiodactyla (0.396 & 0.198 respectively; Appendix table 2) and the average weight of wildebeest (208 kg) (Robinette 1963; Talbot & Talbot 1963; Sachs 1967; Dorst & Dandelot 1970; Delany & Happold 1979; Damuth 1987; Kingdom 1997; Stuart & Stuart 1997).

This value is converted into a daily megajoule equivalent using equation 5.5, where *W* is the average weight of an animal in grams and the energetic equivalent of oxygen (*EO*) is 20.1 KJ/l O_2 (Blaxter 1989). For an average wildebeest (221 kg), this provides a figure of 23.21 MJ/day.

$$BMR = \frac{\frac{24(a + (-b)Log_{10}(W))^{10}W}{1000}EO}{1000} \qquad (5.5)$$

As BMR is only the rate at which energy must be released metabolically in order to maintain an animal at rest, it needs to be converted into realised metabolic rate (RMR). This takes into account the average metabolic requirement for daily activities like moving, ruminating and foraging. Peters (1983) estimated that RMR ranges from 2.6 to 3.5 times BMR, although generally BMR is multiplied by 3, as it is considered an average (used by Lamprey 1964; Eltringham 1974; Coe *et al.* 1976; Wilmshurst *et al.* 1999a). This average is, therefore, used to estimate the RMR of species in the model. For example, the average wildebeest is estimated to have an RMR of 69.62 MJ/day. To test the accuracy of the estimated RMRs, examples of actual RMRs for Artiodactyla species can be used as a comparison (Figure 5.4).

An analysis of covariance, showed that there was a significant difference in the relationship between body weight and RMR between sourced data and that calculated using Hayssen & Lacy's (1985) equation, (F value = 4.651, $P < 0.05$).

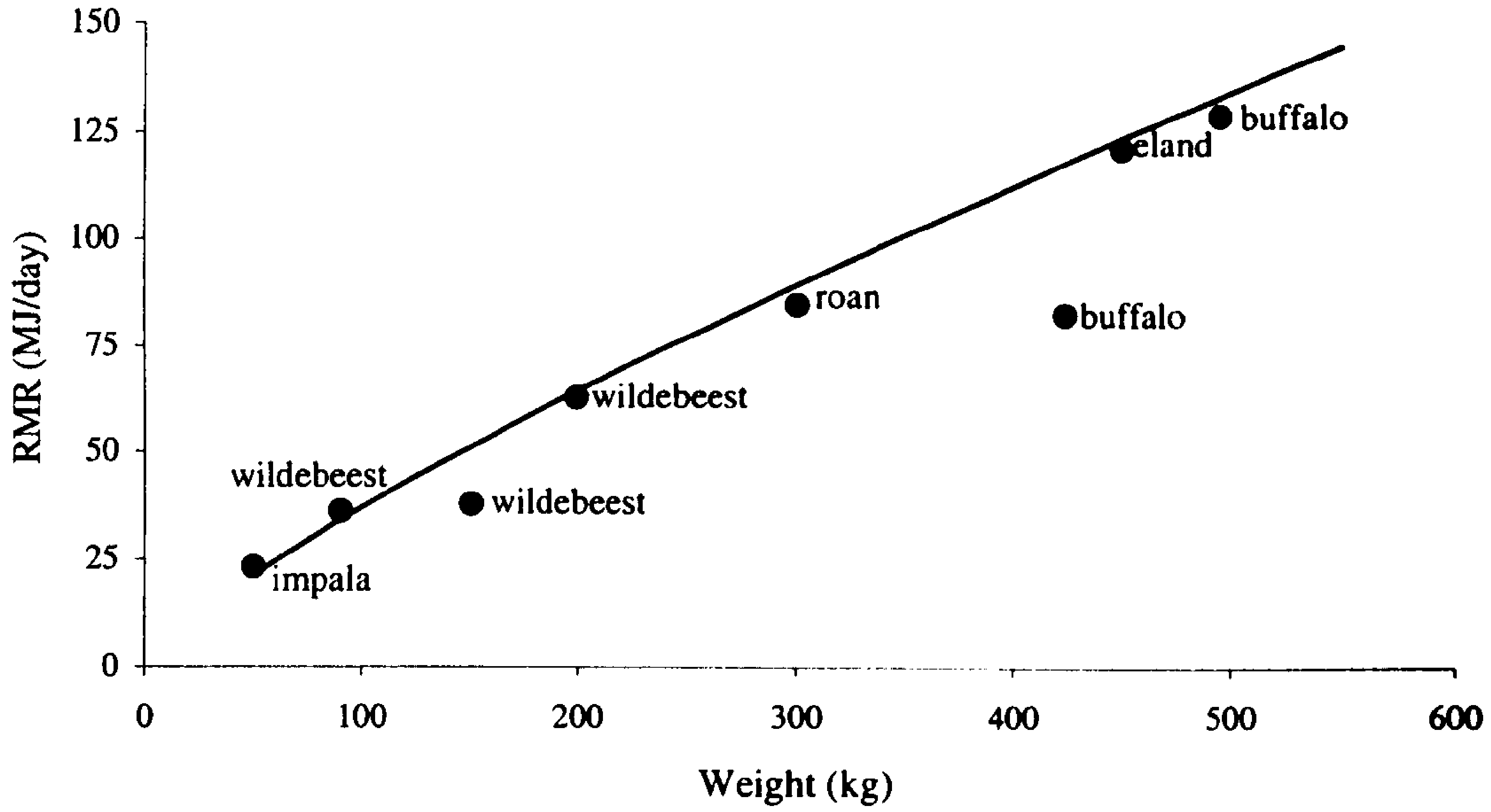

Figure 5.4 Comparison between RMRs for various herbivores from the Order Artiodactyla given by Rogerson (1966, 1968), Sinclair (1974d), Gander (1982) and Wilmshurst *et al.* (1999a) (dots) and RMRs estimated using Hayssen & Lacy's (1985) equation (line).

Interestingly, the two points that appear to be outliers in figure 5.4, are from Sinclair (1974d). He refers to these figures as 'metabolic energy expenditure', and were initially assumed to be RMR values. In retrospect, these could be resting (standard) metabolic requirements (SMR), commonly measured when it is impractical to acquire BMR equivalents (Blaxter 1989). The range of SMR tends to be 2 to 3 times BMR, depending on the food material an animal processes (Blaxter 1989). Sinclair's data does correspond with this, as both figures fall into this range when compared to equivalent BMRs calculated using Hayssen and Lacy's equation. In light of this, the ANCOVA was repeated with Sinclair's data points omitted. This time, the sourced data and the estimated figures did not significantly differ from each other ($F = 3.553$, $P > 0.05$). Hayssen and Lacy's equation can therefore be used with confidence.

5.3.2 Thresholds and variation within a population

At this point, various *FpA* values (energy available) and the average RMR for a wildebeest (energy required) can be used to construct a simple survival curve. This implies that when *FpA* ≥ RMR wildebeest survive, but when *FpA* < RMR they die (Sinclair 1974d). This acute threshold results in a sudden switch from 100% survival to 0% survival (Figure 5.5a).

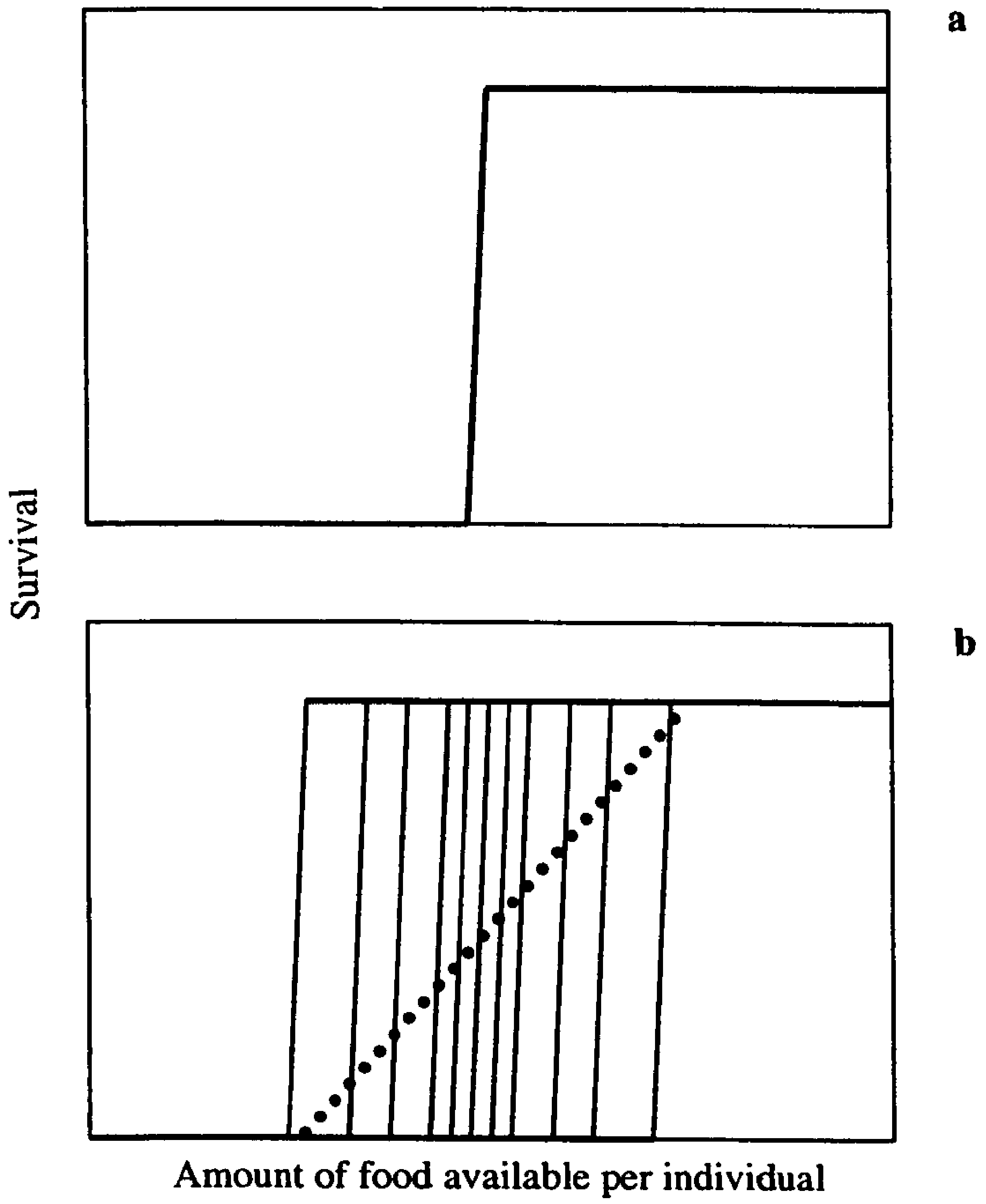

Figure 5.5 Diagram illustrating (a) survival if all individuals within a population are the same, and (b) the range of survival if individual variation is included. The dotted line indicates the population curve.

In practice this abrupt conversion is unlikely, simply because both *FpA* and RMR vary (Young 1994). RMR varies because weight varies and *FpA* varies because foraging ability varies (Western 1979; Kirkwood 1983; Weiner 1992). Consequently, this individual variation gives a whole range of 'sudden curves', which at a population level, results in a gradual conversion from 0% survival to 100% survival (Goss-Custard & Durell 1988; Illius *et al.* 1995; Figure 5.5b).

5.3.2.1 *Variation in RMR due to variation in weight*

Metabolic rates are related to body size, in that the larger the animal, the more energy it requires, and this is reflected in the amount of food it needs (Blaxter 1989). Since body weight varies between individuals within a population, so will food requirements. A range of RMRs, based on body size can, therefore, be used to introduce variation into a population. Although detailed information on body weight distribution is lacking for the Serengeti species, it seems reasonable that it will follow a normal distribution according to the Central Limit Theorem (Sokal & Rohlf 1995). Essentially, this states that when the means of a large number of samples are drawn randomly from the same population, they are normally distributed around the population mean, μ.

Robinette (1963) does, however, provide body weight data for buffalo (*Syncerus caffer*), lechwe (*Kobus lechwe*), bushbuck (*Tragelaphus scriptus*) and warthog (*Phacochoerus aethiopicus*) in Zimbabwe, and Coulson (1989) gives body weights for pangolin (*Manis temmincki*). These were analysed using SPSS (1998) in order to test for normality, and the results are shown in table 5.1. There can be two measures of departure from normality. The first is skewness, where one tail of the curve is drawn out or skewed more than the other. A negative value indicates skewness to the left and a positive value indicates skewness to the right. The second departure from normality is kurtosis. This is a measure of the 'flatness' of the distribution, which can differ from normal by either being leptokurtic or platykurtic. A leptokurtic distribution, indicated by a positive value, has more samples in the mean and tails, while a platykurtic distribution, a negative value, has more samples in the 'shoulders' of the distribution (Sokal & Rohlf 1995).

Table 5.1 Analysis of weights given by Robinette (1963) for African mammals in Zimbabwe, including buffalo, lechwe, bushbuck and warthog, and Coulson (1989) for pangolin. A *t* test (* indicates that $P > 0.05$, is therefore significant) and a Kolmogorov-Smirnov test (** indicates significance, as $P < 0.05$) test for any departure from normality.

	Pangolin	Lechwe	Buffalo	Bushbuck	Warthog
Total Number	28	18	16	20	31
Mean (SE)	7.74 (0.69)	95.54 (3.68)	551.38 (28.51)	34.76 (1.86)	71.76 (2.71)
Std. Deviation	3.66	15.61	114.03	8.32	15.09
Kurtosis (SE)	0.12 (0.86)	-0.58 (1.04)	-1.08 (1.09)	0.18 (0.99)	-0.81 (0.82)
Skewness (SE)	0.93 (0.44)	-0.32 (0.54)	0.18 (0.56)	0.91 (0.51)	-0.17 (0.42)
t-test for kurtosis	0.14	0.56	0.99	0.18	0.98
t-test for skewness	2.10*	0.59	0.32	1.77	0.40
Kolmogorov-Smirnov Z test	0.86	0.68	0.51	0.9	0.54

The tests in table 5.1 reveal that all body weight distributions are not significantly different from normal, except the *t* test for the pangolin, which indicates a significant skew to the right.

As these data sets are rather small, the general lack of significance from a normal distribution may be due to the low power of the tests (Sokal & Rohlf 1995). That is, the tests ability to distinguish the observed data from a normal distribution is poor (Cohen 1988; Quinn & Keough 2002). Table 5.2 illustrates the two types of error that may occur when sample size is too small.

Table 5.2 The different outcomes of a statistical test that can occur when sample size is too small (Cohen 1988).

		Hypothesis	
		H_0 that normal distribution occurs	H_1 that normal distribution does not occur
Outcomes	H_0	correct acceptance	type II error β
	H_1	type I error α	correct rejection

Here, a type I error represents a 'false positive', while a type II error is a 'false negative'. To test the likelihood of either of these being an outcome, a power analysis can be carried out (Cohen 1988). This tests the power of a sample by assuming that as sample size increases, the sample statistic will approach that of a normal distribution, i.e. $H_0 : m = c = 0$, (Sokal & Rohlf 1995). m is the sample statistic and c is the value specified by the null hypothesis. Cohen (1988) states that to determine the proportion of deviation away from the normal distribution (d_3^1), equation 5.6 is used. Here, σ is the population's standard deviation and m is the value of either kurtosis and skewness (Table 5.2).

$$d_3' = \frac{m-c}{\sigma} \tag{5.6}$$

Based on a survey of the behavioural and psychological literature, Cohen (1988) proposed arbitrary values of 0.2, 0.5 and 0.8 could be used as benchmarks to gauge the probability that neither a type I or II error had occurred. He also acknowledged the user must decide what is acceptable (Quinn & Keough 2002). Table 5.3, shows $P < 0.2$ for all the distributions, except pangolin, where $P < 0.5$. This clearly indicates the power of all the samples used is too small to determine whether they follow a normal distribution.

Table 5.3 Proportion of deviation from a normal distribution for both measures of normality, kurtosis and skewness, calculated from the distribution of weight in five African species. Where * = $P < 0.2$ and ** = $P < 0.5$.

	Skewness	Kurtosis
Pangolin	0.355**	0.044*
Bushbuck	0.153*	0.029*
Buffalo	0.002*	0.004*
Lechwe	0.028*	0.052*
Warthog	0.016*	0.075*

Despite this, it seems reasonable to assume that body weight is normally distributed. The five small data sets illustrated here do not contradict this view, although the power to detect the departure from normality is low. Therefore, normally distributed variation is used in the model to introduce variation in RMR.

In a normal distribution, there is a tightly defined relationship between the mean (μ) and the units of standard deviation (σ). For example, μ ± 2σ encompasses 68.25 %, μ ± 2σ encloses 95.45% of the population and μ ± 3σ encompasses 99.73% (Sokal & Rohlf 1995; Figure 5.6).

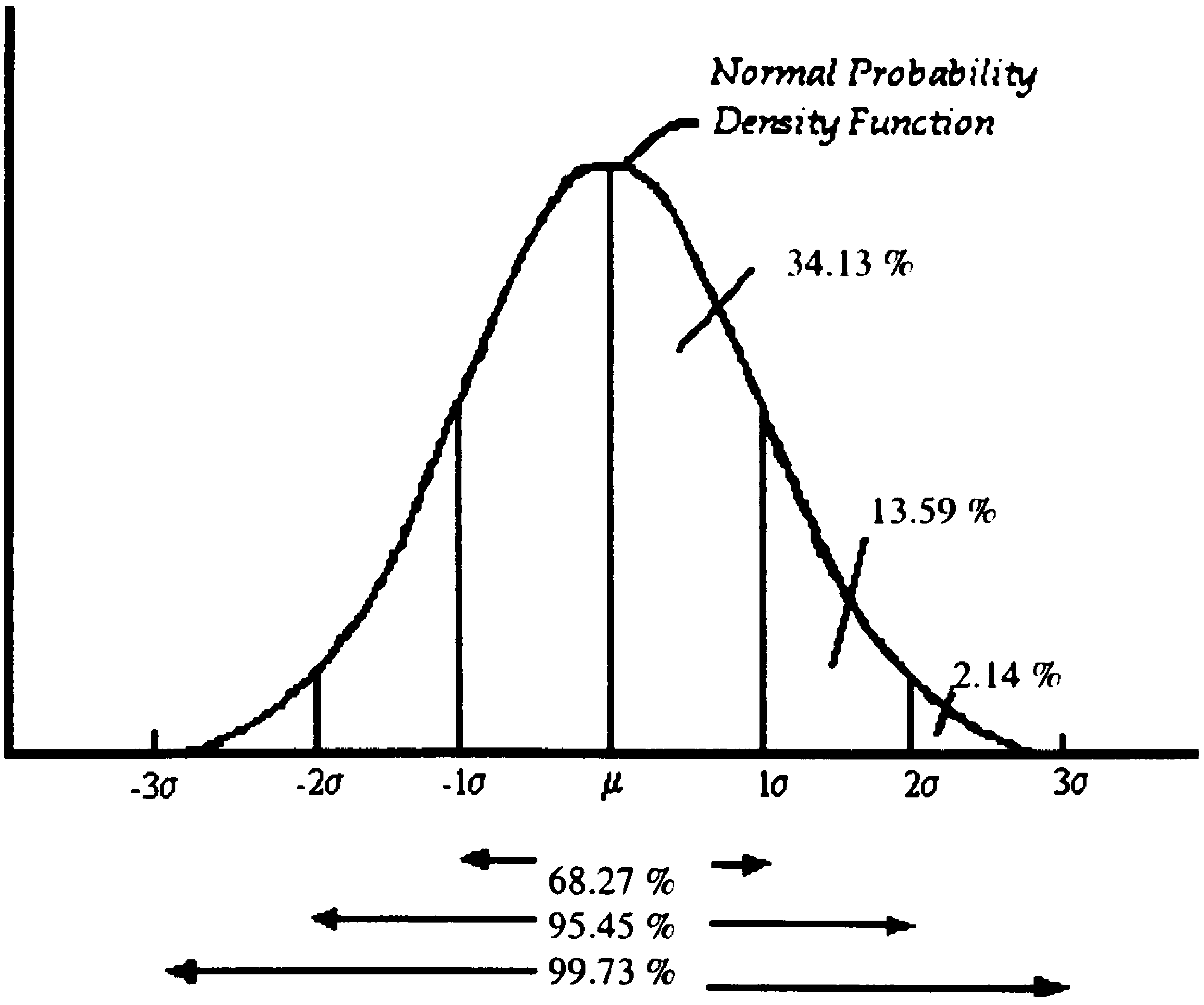

Figure 5.6 A normal distribution curve taken from Sokal & Rohlf (1995)

In order to use the relationship depicted in figure 5.6 to model variation in weight, standard deviations for the body weight of all the species in the model are required. Unfortunately, the only data found in the literature applicable to the model is that for buffalo, analysed earlier in this section (Robinette 1963). An indirect method of estimating standard deviations of body weight is therefore needed. If the weight ranges given by field guides represent the full range of weights found within each species, then these ranges should be approximately equal to six standard deviations (SD), (three either side of the mean, i.e. 99 % of the weights within that population). Unfortunately, the weight ranges given for a particular species differ from author to author. For example, Kingdom (1997) gives a range of 13 kg to 28.7 kg for Thomson's gazelle, while Stuart & Stuart (1997) give a range of 15 kg to 25 kg. However, Stuart & Stuart follow on by saying that gazelle are rarely more then 28 kg, suggesting that gazelles weighing up to 28 kg can be found. It would seem that Kingdom, in this case, gives the largest and the smallest known weights, while Stuart & Stuart give the range that is more likely to be observed. Intriguingly, if it is assumed that Stuart & Stuart's range represents four SD (95% of observations), while Kingdom's range represents six SD (99% of observations), then the weights within each SD are similar.

Because of the differences between field guides high-lighted above, 99 % weight ranges were estimated by taking the smallest and the largest weight that could be found in the literature for each component. For example, the 99 % weight range of adult wildebeest is taken to be 140 kg to 302 kg (with a mean weight of 221 kg), giving an estimated standard deviation of 27 kg (Robinette 1963; Talbot & Talbot 1963; Ledger 1964; Sachs 1967; Dorst & Dandelot 1970; Delany & Happold 1979; Kingdom 1997). The division of wildebeest weight into six weight classes based on these SD is given in table 5.4.

Table 5.4 Division of wildebeest weight range into the six standard deviation units.

	Weight classes					
Minimum weight in kg	140	167.01	194.01	221.01	248.01	275.01
Maximum weight in kg	167	194	221	248	275	302
Proportion of the population	0.0228	0.1359	0.3413	0.3413	0.1359	0.0228

The mid-point of each weight class, in this table, can then be converted into the corresponding RMRs. This is done using equations 5.4 and 5.5 shown in section 5.3.1 and the coefficients for the Order Artiodactyla given by Hayssen & Lacy (1985) in appendix table 2. The next step is to calculate the amount of food necessary to meet RMR and this is dependent on the energy content of a particular resource (Golley 1961; Petrusewicz & Macfadyen 1970; Sinclair 1974d, 1975; Prins & Olff 1998). For example, the sole resource for wildebeest is green grass (Talbot & Talbot 1963; see section 4.4.1), which has an energy content per kilogram of 17.1 MJ (Golley 1961; Robbins 1983; Sinclair 1975; Wilmshurst *et al.* 1999a). However, not all this energy goes towards meeting metabolic demands, as Rees (1978) explains

Intake energy	=	Digestible energy (DE)	=	Metabolizable energy (ME)	=	Basal energy (BE)
		+		+		+
		faeces		urine & methane		activity, growth & reproduction

It is the amount of ME consumed that determines whether RMR is satisfied (de Vos 1969; Theriez & Brelurut 1994). To calculate the ME in 1 kilogram of a particular resource the following equations can be used (Murray 1991);

$$\text{ME (MJ kg}^{-1}\text{)} = 0.0111\ NCD\ (\text{g kg}^{-1}\ \text{DM}) + 3.24 \tag{5.7}$$

Where *NCD* is the neutral detergent cellulase digestibility. However, the appropriate *NCD* values for green grass, are not generally given, instead most authors have quoted crude protein (*CP*) measurements. Fortunately, Murray (1991) also has also determined the relationship between *CP* (g) and *NCD* (g) in his investigation of grasses in the Serengeti National Park, finding that;

$$NCD(\text{g}) = \frac{CP(\text{g}) + 71.8}{0.308} \tag{5.8}$$

Of course, the next step is to find a *CP* value that appropriately represents Serengeti green grass, taking into account that *CP* content can vary between the different types of grassland (Bell 1969; Braun 1973; Afolayan & Fafunsho 1978). For instance, in long grasslands, *CP* was found to be 0.13 kg per kilogram of grass during its first week of growth, while in intermediate grassland, this is 0.16 kg and in short grassland, 0.14 kg (Braun 1973; Duncan 1975; Sinclair 1985). As previously discussed in section 4.4.1, as grass matures, *CP* drops to 0.04 kg, at which point it becomes dry grass. Consequently, at any one time, there will be a variety of grasses at different levels of maturation. Therefore, it is assumed that a mid-range *CP* value would adequately represent the average foraged by a non-selective grazing herbivore. Hence, *CP* in long grassland is 0.085 kilograms per kilogram of grass, intermediate is 0.1 kg and short is 0.09 kg. Using equations 5.7 and 5.8, the green grass in long, intermediate and short grasslands were estimated to have ME values of 8.89, 9.43 and 9.07 MJ/kg, respectively.

Obviously, the more ME in a particular type of food, the less an animal needs to consume to meet its metabolic requirements (Afolayan & Fafunsho 1978). By migrating, wildebeest occupy the long grasslands of zone 1 in the dry season, where they receive approximately 8.89 MJ of metabolizable energy for every kilogram of grass eaten. During their occupancy of zone 3's mixed grasslands in the wet season, they receive 9.13 MJ/kg (an average of the three grassland types). The degree of influence these varying MEs have on population survival can only be determined by comparing the resulting survival curves (see section 5.3.2.2). However, the ME value for green grass in zone 1 will be used initially to construct a survival curve for adult wildebeest. The amount of food (minimum intake) necessary to meet RMR requirements in zone 1 for each weight class is shown in table 5.5.

Table 5.5 Variation in RMR and food requirement within the adult wildebeest population as a result of variation in weight (in zone 1).

	Weight classes					
Mid-point of weight categories (kg)	153.5	180.5	207.5	234.5	261.5	288.5
Daily RMR for weight (MJ)	51.97	59.19	66.19	73.01	79.68	86.21
Equivalent daily intake of food (kg)	3.04	3.46	3.87	4.27	4.66	5.04

5.3.2.2 *Variation in FpA due to variation in foraging efficiency*

Individual variation also occurs in the form of foraging ability (Underwood 1983; Goss-Custard *et al.* 1995a). Some individuals are better equipped or more capable of foraging than others (Seagle & McNaughton 1992; Cuthill & Houston 1997). For example, a study by Ritchie (1988) showed that free-living Columbian ground squirrels, *Spermophilus columbianus,* varied in their ability to maximise daily energy intake. He also noted that these individual differences, which were consistent across seasons and not related to social factors, seemed large enough to have fitness consequences. Sutherland & Dolman (1994) go on to state that the variation in foraging abilities of an individual can influence survival, in that they fail to achieve their minimum intake. Consequently, this reflects on overall population survival. Of course, there are a number of aspects that govern an individual's foraging ability. Some of these are behavioural, such as bite rate, type of forage selected, time spent foraging, foraging area selected, time spent commuting to those areas and in the case of ruminants, time spent ruminating (Stobbs 1973, 1974;

Grimsdell & Field 1976; Murray 1991; Underwood 1983; Gross *et al.* 1993b; Spalinger 1994; Bradbury *et al.* 1996; Shipley *et al.* 1996; Etzenhouser *et al.* 1998; Wilmhurst *et al.* 1999a). For instance, in the case of the Columbian ground squirrel, diet selection appeared to be the major cause of variation between individuals (Ritchie 1988). Then there are the physical aspects that constrain intake rates, such as bite size, retention time (fermentation rate) and total gut capacity (Allden & Whittaker 1970; Underwood 1983; Demment & van Soest 1985; Illius & Gordon 1992, Gross *et al.* 1993b; Spalinger 1994; Bradbury *et al.* 1996; Wilmshurst *et al.* 1999b; Twine 2002). For example, differences in the breadth of the incisor arcade in overwintering Soay sheep, *Ovis aries*, were found to have clear fitness consequences (Illius *et al.* 1995; Goss-Custard & Sutherland 1997).

To determine the effect of foraging variation amongst individuals on overall population survival, information on all these aspects needs to be incorporated into the model. Surprisingly, very little information on the behavioural aspects of foraging variation has come to light. One such study was carried out by Stobbs (1974) to investigate grazing behaviour in dairy cows. However, although this revealed that there are behavioural variations between individuals in a population in terms of bite rate, only a very tenuous link can be made between Stobbs' data and wildebeest. Alternatively, there are a number of studies that have yielded a range of stomach fills for various African species (Table 5.6). Such ranges indicate that different intake rates can occur amongst similar sized individuals and thus demonstrates that foraging decisions can vary.

Table 5.6 Range of stomach fills as a percentage of live weight, measured from a number of sampled populations.

Reference	Species	Percentage of body weight		
		Minimum stomach fill	Maximum stomach fill	Range
Talbot & Talbot 1963	Wildebeest	7.60	14.70	7.10
Mundy *et al.* (1983)	Impala	3.50	7.00	3.50
Buss 1961	Elephant	0.30	6.00	5.70
Laws & Parker (1968)	Elephant	0.22	6.25	6.03
Laws & Parker (1968)	Elephant	0.82	4.07	3.25

Table 5.6 shows that amongst the different samples there is a great deal of variation, even between the same species. For instance, Laws & Parker (1968) sampled two elephant populations in Murchison Falls National Park, Uganda, separated only from each other by the Victoria Nile. Yet, they found that the stomach fill range of one population was almost twice that of the other. The overall inconsistency between the samples in table 5.6, makes it difficult, not only to select a stomach fill range representative of the Serengeti's migratory wildebeest population, but also estimate ranges applicable to all the other components in the model. Therefore, a sensitivity test was carried out to analyse the effect of applying various stomach fill ranges, as indicators of foraging efficiency, on population survival.

To do this, it was first assumed that stomach fill (S) represented daily intake (I), i.e. S depicts the amount of forage accumulated in the stomach in one day. Consequently, stomach fill range span (distance between one foraging extreme to the other) was equal to the daily intake range span ($S_R=I_R$). A variety of plausible I_R values were then chosen using the samples given in table 5.6 as a general guide. Amongst the S_R values given, none exceeded 7.5 % of body weight. A feasible explanation for this is that absolute maximum intake rate is limited by an animal's physiology (Demment 1982; Demment & van Soest 1985; Damuth 1987). Furthermore, it was assumed, unless otherwise stated, that the S_R values were wet weight measurements. If these are converted, the samples in table 5.6 do not exceed 2.3 % or fall below 1 % of body weight. This is relatively similar to Sinclair's (1974a, 1975) prediction that the dry weight intake range of dominant herbivores is 1.5 % of body weight and Prins & Douglas-Hamilton's (1990) quote of 2.5% body weight. As *FpA* and minimum intake (I_M) are dry weight values in the model, the S_R values, therefore, chosen were based around this dry weight variation amongst the samples in table 5.6. Hence, a range of 1 %, 2 % and 3 % of body weight (0.01 W, 0.02 W & 0.03 W) were selected, where the mean weight of an individual in a specified population was used. For example, as the mean weight of wildebeest is 221 kg, these ranges worked out to be 2.21 kg, 4.42 kg and 6.63 kg, respectively.

Within the model, it was assumed that these S_R values (therefore I_R values) were a set range. In other words, those individuals at the higher end of the range will always get *n* kg more forage then those at the lower end of the range. It was further assumed that *FpA* corresponded with the average amount of food that can be foraged by an individual and this was taken to be the mid-point of each I_R. Consequently, individuals with efficiencies above or below the mid-point exhibit intakes that are $I>FpA$ and $I<FpA$, respectively. The proportional distance (I_RP) from the mid-point can then be used to calculate the amount of

food consumed above or below *FpA* by individuals lying at specific points along the I_R (Figure 5.7).

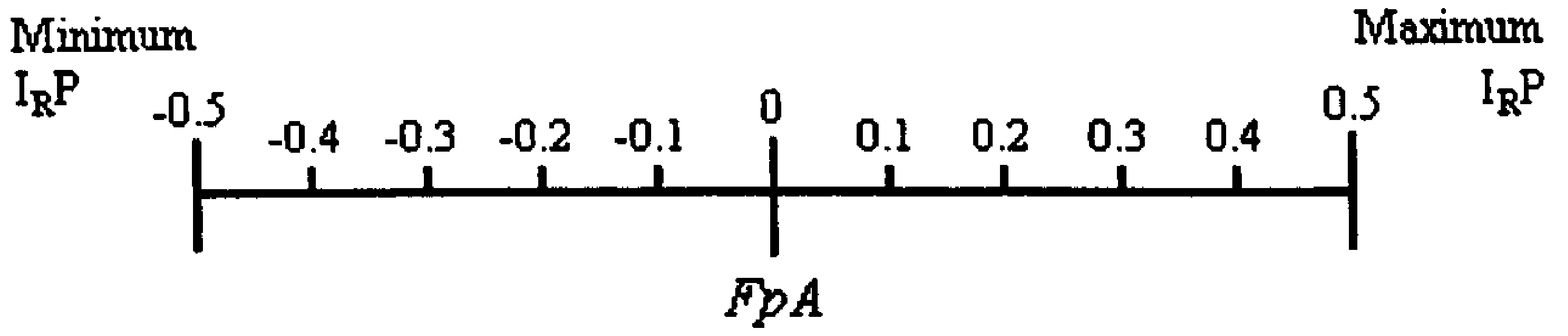

Figure 5.7 Illustration to show intake range span symmetrically distributed around *FpA*. The proportional distance from the mid-point of the intake range span represents the amount of food in kilograms consumed above and below *FpA*.

When these supplementary amounts are added to *FpA*, the daily intake of such individuals can then be determined. This is expressed in the following equation,

$$I = FpA + (I_RP(I_R)) \tag{5.9}$$

At this point, another assumption needs to be made about the distribution of individuals within this range. In a study to investigate whether the specific combination of foraging efficiency and dominance in individual oystercatchers (*Haematopus ostralegus*) affected their chance of survival in the Exe estuary in England, Clarke & Goss-Custard (1996) believed that individual foraging efficiency, as a continuous variable, would be normally distributed. Assuming this is the case, I_RP can be divided equally into six standard deviations (foraging classes; Figure 5.8) with the proportion of individuals distributed normally in each, as given in table 5.4.

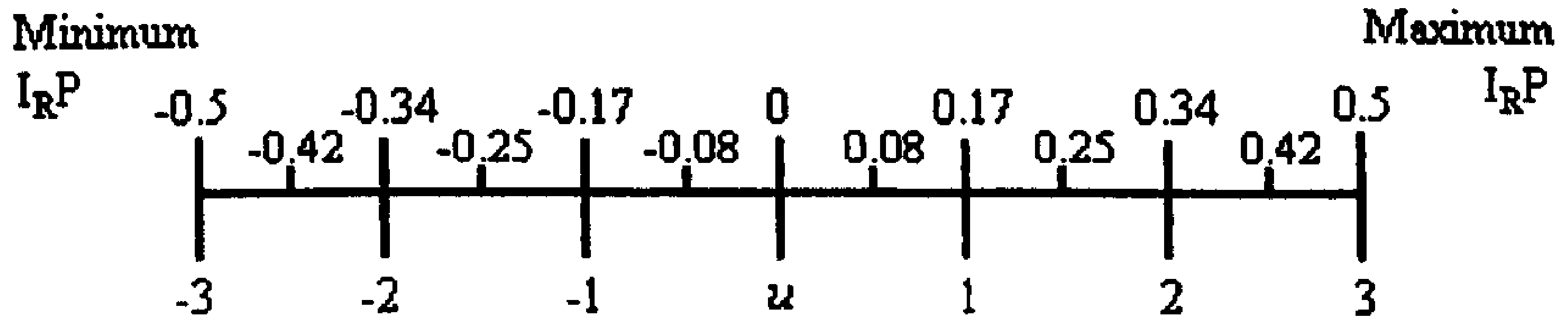

Figure 5.8 Proportional distance at each foraging class limit and mid-point along intake range span.

If the mid-point of each foraging class is taken to represent the average amount of food foraged by individuals within it, then the I_RP at these points can be used to estimate the average intake within each class for a specified *FpA* (Figure 5.8). However, this intake value does not consider that foraging ability is also physically constrained by factors such as bite size, gut capacity or retention time (Underwood 1983). For instance, two individuals may be equally efficient, but variations in their physiology will vary their intakes. Therefore, by including these physical variations, the survival of a population as a result of foraging efficiency and capability can be determined.

Fortunately, unlike the behavioural aspects, more information is available on intake rates affected by physiology. In fact, a number of studies confirm that physiological characteristics are generally related to body mass (W) (Demment 1982; Demment & van Soest 1985; Damuth 1987). Bite size ($W^{0.72}$ DM g), gut capacity (rumen capacity of grazers 25.6 W DM g) and retention time (for hindgut fermenters 9.4 $W^{0.255}$/hr and 15.3 $W^{0.251}$/hr in ruminants) will, therefore, be relatively similar amongst similar sized individuals (Illius & Gordon 1987, 1992; Shipley *et al.* 1994; Spalinger 1994). As previously discussed in section 5.3.2.1, the wildebeest population has a range of weights and inevitably, the degree of physiological variation incorporated depends on the extent to which this weight range is apportioned. Therefore, for convenience, the weight classes used in the previous section could be applied here (table 5.5). The appropriate bite size, retention time and gut capacity for each weight class could then be used to calculate maximum intake rates. However, in the previous section, a range of I_M values corresponding to the weight range have already been calculated (table 5.6). It can, therefore, be assumed that the distance from the smallest to the largest I_M is a reflection of the physiological variation within a population (B_R). For wildebeest, as I_M ranges from 2.82 to 5.23 kg/day (see sections 5.3.1 & 5.3.2.1), B_R is 2.42 kg (5.23-2.82).

As it happens, B_R represents a parameter with similar characteristics to I_R and as such, can be utilised in the same way. For instance, if in equation 5.9, I_R is replaced by B_R, the intake of a particular sized individual can be calculated. Furthermore, as B_R mirrors weight range, it will have a normal distribution with similar standard deviations. Consequently, the average amount of food individuals are physically capable of foraging in a particular weight class (*FpWC*) can be calculated.

$$FpWC = FpA + (I_R P(B_R)) \tag{5.10}$$

I_R can then be applied to each weight class, in which individuals with an average foraging efficiency will have intakes equal to *FpWC*. Equation 5.9 is, therefore, modified to:

$$I = FpWC + (I_R P(I_R)) \tag{5.11}$$

The result is that for each of the six weight classes there will be 6 foraging classes, for which an average intake value is estimated. These can then be compared with the minimum intake requirement (I_M) for wildebeest in that weight class, given in table 5.5. Where I_M is met, the individuals within that foraging class survive. Overall population survival can be determined by combining the proportion of individuals within each surviving foraging class. For example, the proportion of individuals in the smallest foraging class and in the smallest weight class is equal to 0.05 % of the total population (2.28 % of 2.28%).

By estimating overall population survival for a variety of *FpA* values, a survival curve can be created by plotting percentage survival against *FpA*. The different I_R values selected can then be applied (2.21 kg, 4.42 kg and 6.63 kg), and the resultant curves compared. Figure 5.9, reveals that each resembles an S-shaped curve, unlike the curve created by the Holling type-II functional response used by Hilborn & Mangel (1997) in figure 5.3. Moreover, varying I_R, varies the slope of the middle section of the curve. By increasing I_R the slope becomes less steep, indicating a greater variation in survival between different weight and foraging classes within the population. The question is, which curve adequately represents the degree of variation that exists in a natural wildebeest population? Without sufficient empirical data it is very difficult to make an educated guess. In fact a simpler option for the model would be to incorporate the variation in RMR between individuals alone.

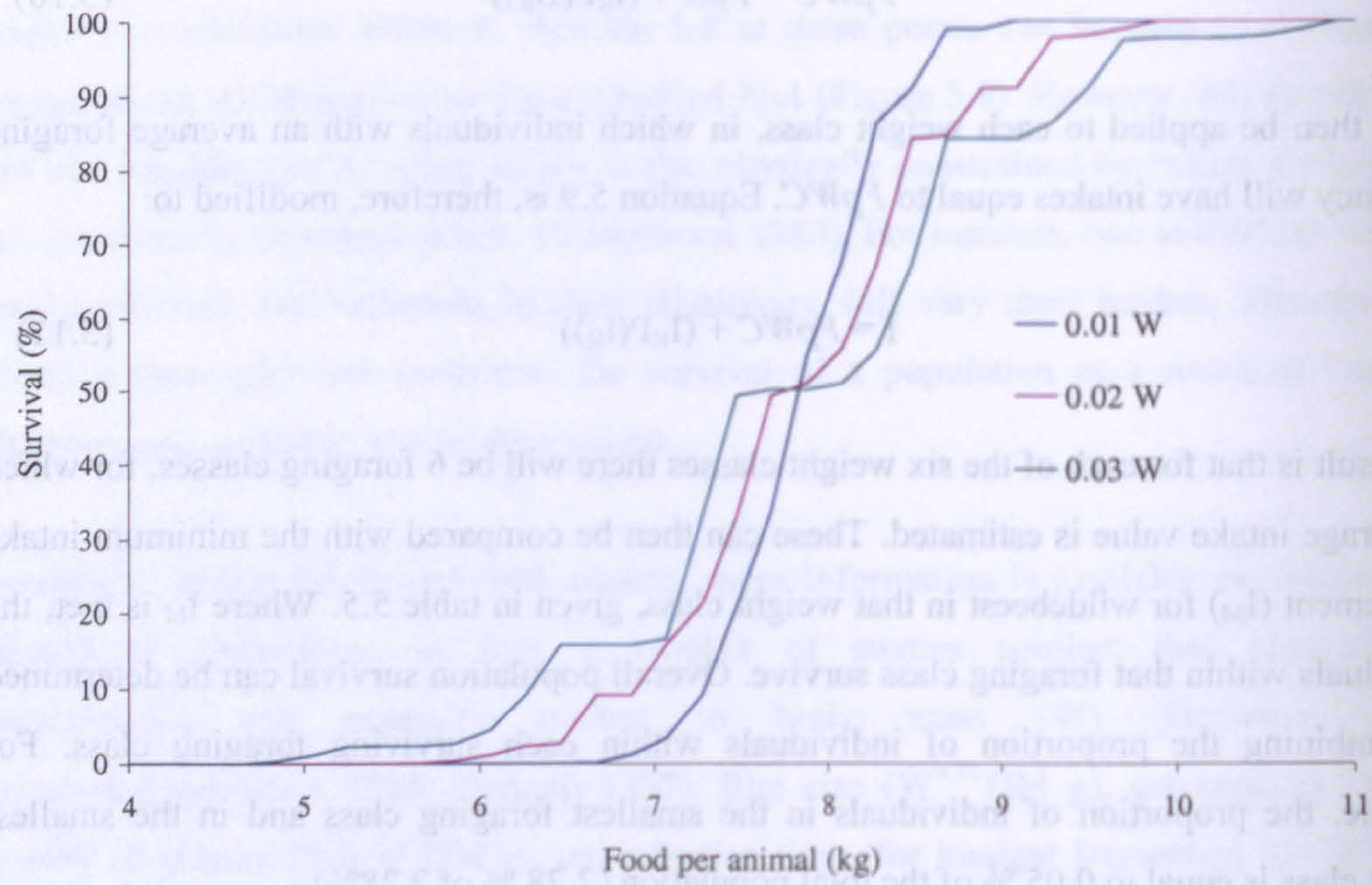

Figure 5.9 Survival curves produced when the daily intake range spans 1 %, 2 % and 3 % of body weight (kg).

By comparing the average I_M of each weight class with *FpA*, an alternative survival curve can be created. That is, if $FpA \geq I_M$, then the individuals within that class survive and the total proportion of individuals to survive equals overall population survival. However, with only 6 weight classes and subsequently seven data point positions, the shape of the curve is not well defined. This can be rectified by further sub-dividing the weight classes. The distribution of individuals within each sub-class can be found by using the Z values (the normal deviate) that correspond to each class limit (i.e. -3, -2.75, -2.50 etc; Zar 1999; see section 5.3.2.1). The proportion of individuals that lie beyond each Z value (therefore, class limit) are given in standard statistical tables for the proportions of a normal curve. By taking one proportion from the next, the distribution of individuals in each sub-class can be calculated (Appendix table 3). These weight classes, their average I_M values, and the proportion of the population each represent, can then be used to estimate survival (Figure 5.10).

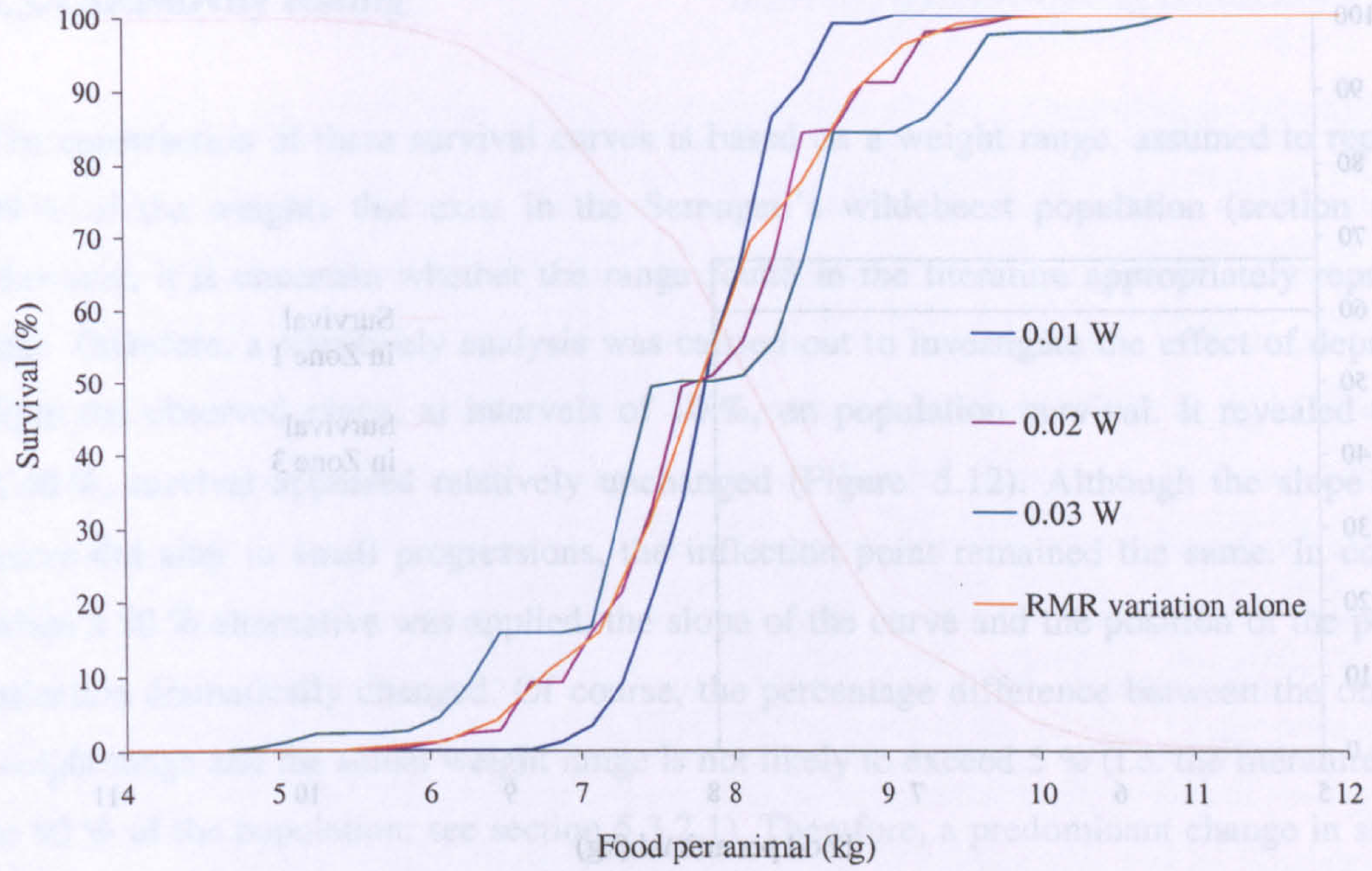

Figure 5.10 Survival curves produced when foraging efficiency is included with various intake range spans and when RMR variation is used alone.

The survival curve produced is once again a well-defined 'S' shaped curve. In fact, when superimposed upon the previous survival curves (Figure 5.9), it is virtually identical to that with a range span equal to 0.02 W. This implies that using RMR variation and foraging variation with this range span achieves no more variation than if RMR variation were used alone. Although this does not condemn the use of foraging variation, it reinforces the decision not to use it in the model.

5.3.3 Zonal influence on survival

As previously discussed in section 5.3.2.1, the metabolic energy provided in a kilogram of green grass varies between zones. Comparing the adult wildebeest survival curve produced for zone 1 with that of zone 3 reveals a substantial degree of variation (Figure 5.11). This indicates that the zone wildebeest occupy in a particular season influences their seasonal survival. For example, when FpA = 8 kg, 59.9 % of adult wildebeest survive in zone 1, compared to the 69.2 % in zone 3. This represents a difference in the life or death of 10 % of the population.

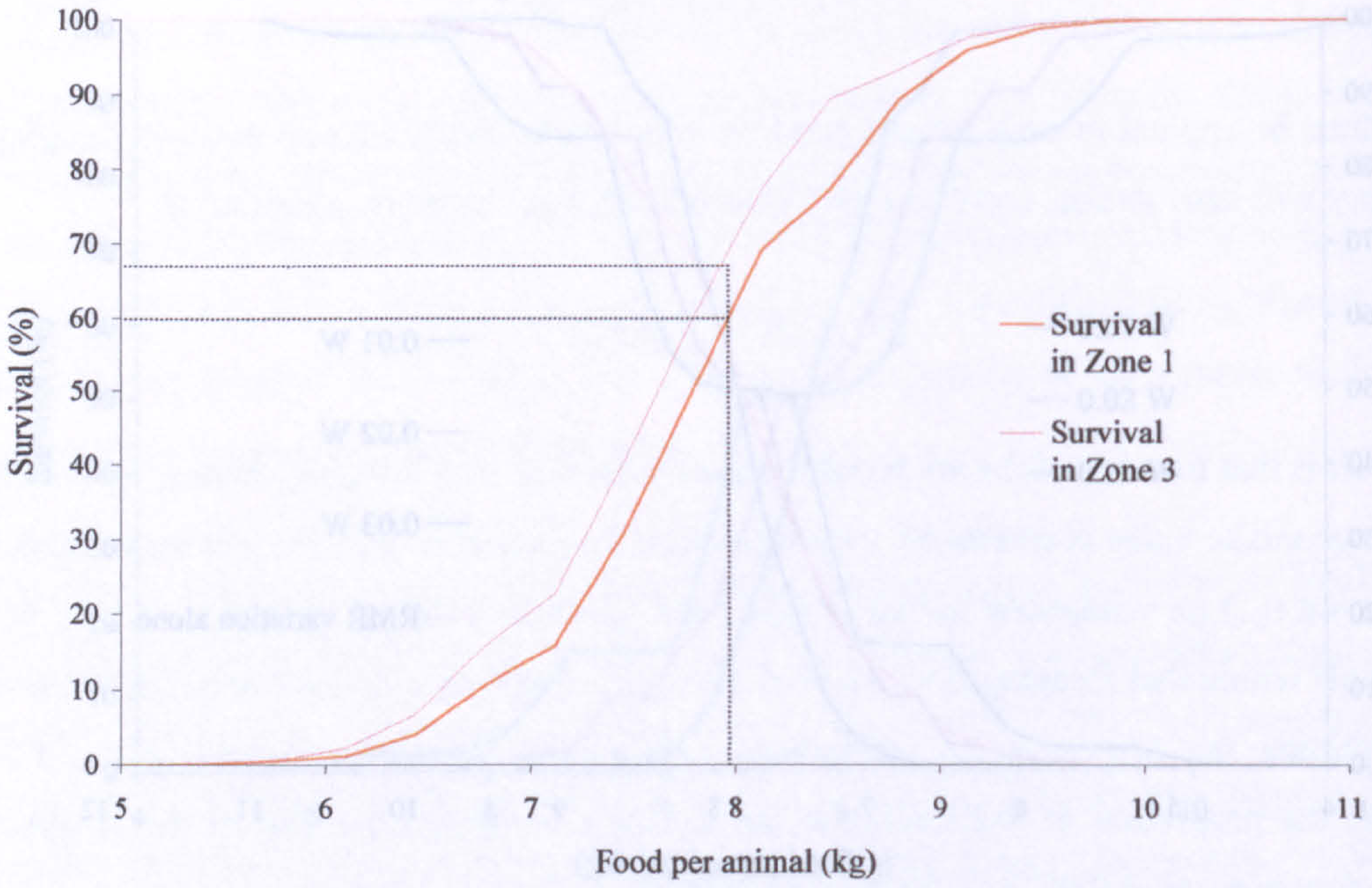

Figure 5.11 Survival curves produced when the ME content of green grass in zone 1 and zone 3 are applied. Dotted black line shows the percentage of population to survive when *FpA* = 8.

Interestingly, during the migration from each zone, wildebeest incur a proportion of accident-related mortality. For instance, large numbers of wildebeest drown or get trampled during river crossings (Talbot & Talbot 1963, Turner 1987). Talbot & Talbot (1963) estimated that this constituted 16.2 % of wildebeest mortality, with 94 % involving adults and 6 % young (Figure 5.12). They also estimated that 36.5 % of mortality was due to predation and 5.85 % of the total population, including young, succumbed to predation each year. Therefore, accident-related mortality would constitute 2.6 % of the total population annually ([5.85/36.5] x 16.2), 2.4 % of adults ([2.6/100] x 94) and 0.2 % young. This is supported by Wolanski *et al.*'s (1999) statement that migratory wildebeest have 3 % more annual mortality compared with resident populations. The difference between 3 % mortality incurred during migration and the 10 % brought about when $FpA < I_M$ in zone 1, may to some extent justify the manifestation of migration, or at least the migratory wildebeest's high abundance (Wilmshurst *et al.* 1999b). Furthermore, as this indicates the quality of the food eaten is a critical factor in affecting species productivity, separate survival rates for each zone should be included in the model (Blaxter 1962; Stanley-Price 1978).

5.3.4 Sensitivity testing

The construction of these survival curves is based on a weight range, assumed to represent 99 % of the weights that exist in the Serengeti's wildebeest population (section 5.3.2). However, it is uncertain whether the range found in the literature appropriately represents this. Therefore, a sensitively analysis was carried out to investigate the effect of departures from the observed range, at intervals of 10 %, on population survival. It revealed that at ≤ 40 %, survival appeared relatively unchanged (Figure. 5.12). Although the slope of the curve did alter in small progressions, the inflection point remained the same. In contrast, when a 50 % alternative was applied, the slope of the curve and the position of the point of infection dramatically changed. Of course, the percentage difference between the observed weight range and the actual weight range is not likely to exceed 5 % (i.e. the literature refers to 95 % of the population; see section 5.3.2.1). Therefore, a predominant change in survival at 50 % is of no concern when observed weight ranges are used in the model.

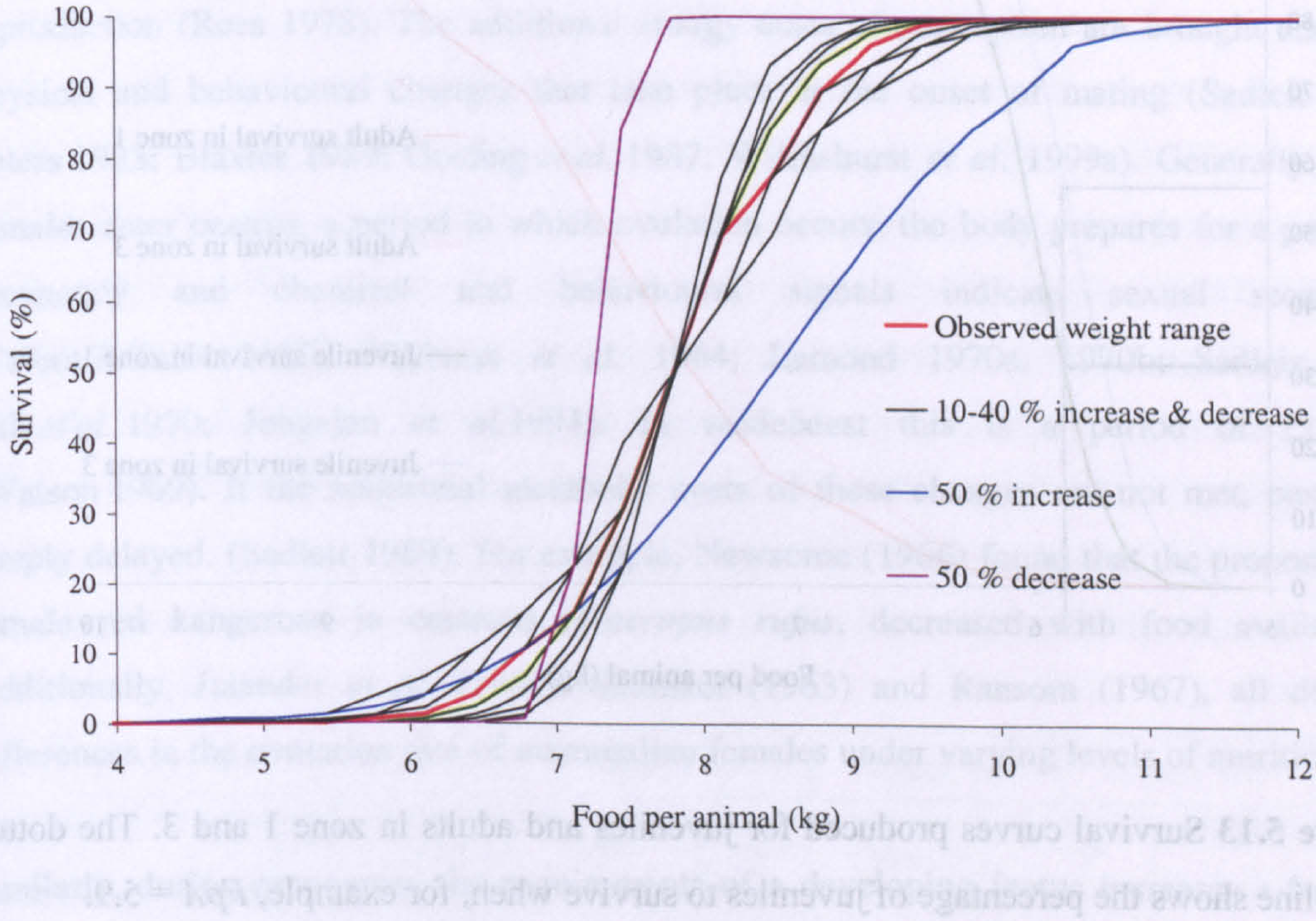

Figure 5.12 Relationship between wildebeest survival and food availability, when weight range is varied systematically.

5.3.5 Functional group-related survival

As body size affects the daily intake of individuals, it seems reasonable to presume that in comparison to adults, both juveniles and young will require less food to survive. Consequently, the position of their survival curves will differ from that of adult wildebeest. Moreover, as their weight ranges are comparatively small (e.g. juveniles only weigh from 136 to 181 kg), so will be their food intakes. This creates a steeper sloping survival curve, as seen in figure 5.13, comparing juvenile to adult survival. These clear variations in survival between functional groups warrant the application of separate survival rates for each within the model. Furthermore, the use of zone-specific survival rates is reinforced, as the ME content of grass strongly influences juvenile survival. For example, when *FpA* = 5.9 kg, 30 % of juveniles survive in zone 1, compared to 59 % in zone 3 (Figure 5.13).

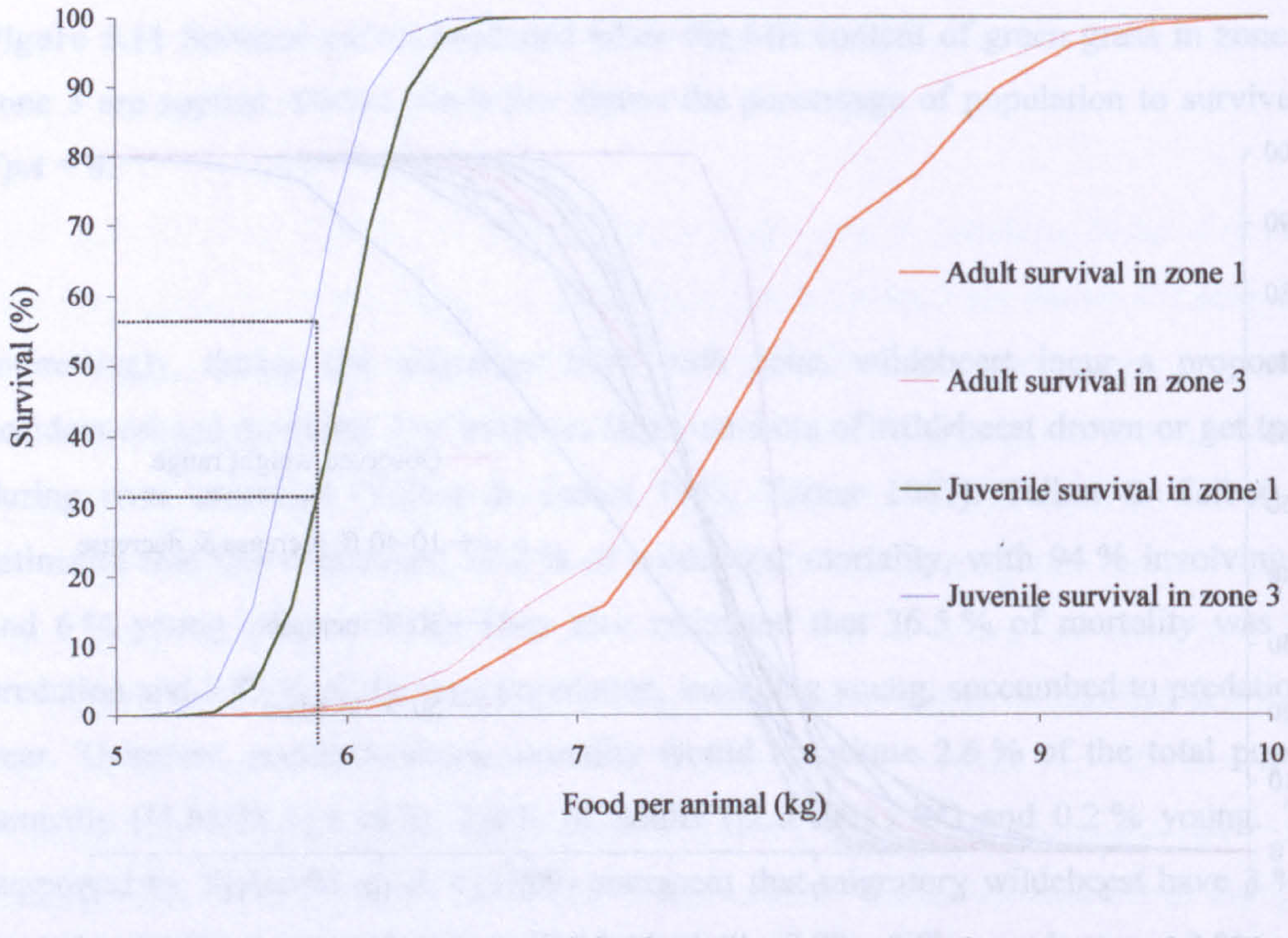

Figure 5.13 Survival curves produced for juveniles and adults in zone 1 and 3. The dotted black line shows the percentage of juveniles to survive when, for example, *FpA* = 5.9.

5.4 PREDICTING RECRUITMENT

Survival, dealt with in the last section, represents one aspect of population dynamics. The other process is recruitment (Watson 1966; Mwangi & Western 1998; Altwegg *et al. 2003*). This can be broadly defined as all those processes which result in the production of young that are eventually capable of breeding (Blaxter 1989). It therefore incorporates conception, birth and survival of young (Watson 1969).

As with mortality, recruitment is dependent on the amount of resource available (Talbot & Talbot 1963; Grodzinski & Goreck 1967; Sadleir 1969; Sinclar 1975, 1977b, 1983; Peters 1983; McNaughton & Georgiadis 1986; Pascual & Hilborn 1995; Mwangi & Western 1998; Prins & Olff 1998; Wilmshurst *et al.* 1999b). Under-nutrition can delay the attainment of puberty, limit conception and affect the birth weight of young during pregnancy (Estes 1966, 1969; Sadleir 1969; Hill *et al.* 1970; Lamond 1970b; Sinclair 1974b; Field 1976; Delany & Happold 1979; Clutton-Brock *et al.* 1987a, 1987b; Blaxter 1989). Furthermore, conception, pregnancy and lactation are dependent on the ability of a potential mother to consume enough food to meet her own metabolic demands and the demands of reproduction (Rees 1978). The additional energy costs of conception are brought about by physical and behavioural changes that take place at the onset of mating (Sadleir 1969; Peters 1983; Blaxter 1989; Gosling *et al.* 1987; Wilmshurst *et al.* 1999a). Generally, when females enter oestrus, a period in which ovulation occurs, the body prepares for a potential pregnancy and chemical and behavioural signals indicate sexual receptivity (Talbot & Talbot 1963; Wiltbank *et al.* 1964; Lamond 1970a, 1970b; Sadleir 1969; Hill *et al.* 1970; Jongejan *et al.*1991). In wildebeest this is a period of 15 days (Watson 1969). If the additional metabolic costs of these changes are not met, oestrus is simply delayed. (Sadleir 1969). For example, Newsome (1966) found that the proportion of female red kangaroos in oestrous, *Macropus rufus*, decreased with food availability. Additionally, Julander *et al.* (1961), Sckinkel (1963) and Ransom (1967), all describe differences in the ovulation rate of mammalian females under varying levels of nutrition.

Similarly, during pregnancy, the requirements of a developing foetus increases a female's nutritional needs (Talbot & Talbot 1963; Watson 1966, 1969; Grodzinski & Goreck 1967; Sadleir 1969; Sinclair 1975). Curtailment of food intake at any time during a pregnancy may have detrimental effects on the young (Forbes 1970). For instance, under-nutrition after conception and prior to implantation may lead to embryonic loss or restrict placental development leading to a miscarriage later in the pregnancy (Everitt 1968). In later stages of gestation, poor nutrition strongly influences prenatal growth and development, profoundly affecting postnatal performance (Everitt 1968, Robbins & Robbins 1979; Clutton-Brock *et al.* 1987a). For example, Verme (1965) showed that reducing the intake of white-tailed deer, *Odocoileus virginianus*, decreased birth rate and lowered birth weight and studies by Murphy & Coates (1966) revealed that decreases in birth weight generally lead to mortality at birth or immediately after.

Moreover, the production of large quantities of milk, a highly nutritious resource, undoubtedly places considerable nutritional strain on mothers (Grodzinski & Gorecki 1967; Forbes 1970; Sinclair 1975; Kreulen 1975; McNaughton 1990; Murray 1995). Kaczmarski's (1966) studies on bank voles, revealed that the average calorific intake is 31.4 kcal/day more for lactating females than non-reproducing females. Without an appropriate level of intake, the amount of milk produced diminishes. When this amount no longer supplies enough energy to meet the RMR of young, mortality ensues (Sadleir 1969; Robbins & Robbins 1979; Blaxter 1989).

To incorporate the effects of food availability on recruitment rate into the model, conception, pregnancy and lactation need to be considered separately. Firstly, as each can span one or more seasons, between which food availability varies. For example, wildebeest conceive around May during the wet season (Talbot & Talbot 1963; Fraser 1968; Watson 1969, Sinclair 1977a; Estes 1966). An eight month gestation period then proceeds through that wet season, the following dry season and into the next wet season, (Watson 1966, 1969; Talbot & Talbot 1963; Stuart & Stuart 1997; Kingdom 1997; Estes 1966; Delany & Happold 1979). Consequently, most calves are born around February and they are weaned mid-way through their second wet season (Talbot & Talbot 1963; Estes 1966, 1976, 1991; Watson 1966, 1969, 1967; Fraser 1968; Sinclair 1977a; Stuart & Stuart 1997; Kingdom 1997; Mduma *et al.* 1999; Figure 5.14).

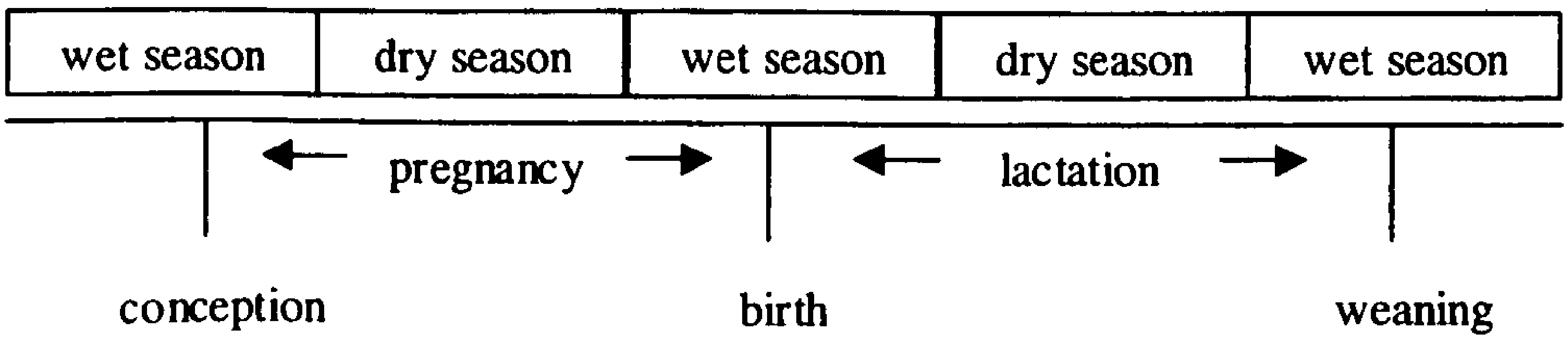

Figure 5.14 Illustration of the timing of reproductive processes in wildebeest.

The second reason for considering conception, pregnancy and lactation separately is because each aspect of reproduction requires a specific amount of energy (Sadleir 1969; Peters 1983). A study by Blaxter (1989) found that for sheep the crude energetic costs for pregnancy, lactation and conception in MJ per day were 2.10, 8.13 and 4.71, respectively. In other words, the success of reproduction is dependent on the amount of food available and the amount of energy needed to achieve or maintain each reproductive process.

5.4.1 Reproductive success

As previously mentioned in section 5.2.1, as only female fertility has a direct influence on recruitment, male reproductive success is not considered here. Therefore, the first step in calculating the recruitment rate is to estimate the number of adult females within the population potentially capable of conceiving. There are two references to the sex ratio of adult wildebeest in the literature. One is by Talbot & Talbot (1963), stating that in the Serengeti-Mara region only 48 % of the total adult population is female and the other is by Sinclair (1977b), who found that the sex ratio of adults was equal on the plains in the wet season. With so little annual information on sex ratios, an alternative method of estimating the number of females in a population was required. Quite simply, the adult functional group was separated into males and females. Survival curves were constructed for both using gender specific weight ranges (e.g.140 to 260 kg for female wildebeest and 165 to 302 kg for males). Consequently, the number of females surviving each season could then be directly linked to recruitment. Furthermore, this also allowed for gender-specific mortality factors to be included into the model, such as predation vulnerability (referred to section 7.7.2; Brooks 1961; Estes 1967; Hvidberg-Hansen & de Vos 1971; Jarman & Jarman 1973; Geist 1974; Kingdon 1982b; Berger 1983b; Gosling 1986; Prins 1989; FitzGibbon 1990; Hack *et al.* 2002; Saltz 2002). However, to initiate the model a 1 : 1 ratio was applied to adult figures in order to make an initial separation, subsequently in the dry season of 1960, 101,798 females were present (50 % of 203,597).

In order to estimate the proportion of females that conceive based on the amount of food available, a recruitment curve relatively similar to the adult survival curves in section 5.3 was constructed. However, there are three modifications to this curve. The first is that the weight range used applies specifically to females (i.e. 140 to 260 kg; Talbot & Talbot 1963; Sachs 1967; Kingdom 1997). The second is that as females only conceive during the wet season, while they are in zone 3, a recruitment curve is only required for that zone (Talbot & Talbot 1963; Watson 1969, Sinclair 1977a; Estes 1966; section 5.3.2.1). Finally, the metabolic requirements of conceiving are added to the RMR of females. Quite simply, if these increased rates are not met by resource consumption it is assumed the female does not conceive.

To calculate this supplementary energy requirement, the information on the crude energetic costs for pregnancy, lactation and conception in sheep previously sited from Blaxter (1989) can be used (2.10, 8.13 and 4.71 MJ/day, respectively). He also states that the daily cost of lactation for a sheep is 0.586 MJ/kg of the mother's metabolic weight. Similar values are given for cow (0.278), horse (0.344), reindeer (0.332), red deer (0.320), goat (0.437) and Dorcas gazelle (0.371). Assuming that the proportional difference between the amount of energy required for lactation and conception is constant between the above species, the daily cost of conception for each can be estimated. For instance, conception costs for a sheep are 0.339 MJ/kgW$^{0.73}$/day ([0.586 / 8.13] x 4.71). Of course, appropriate lactation values are required for the different species in the model. By further assuming that those figures for each species given by Blaxter will be equivalent to taxonomically similar species in the model, the corresponding lactation costs for each can be used. For example, as sheep are most taxonomically similar to wildebeest (Brashares *et al.* 2000), the daily cost of lactation for a wildebeest will be 0.586 MJ/kgW$^{0.75}$/day. The cost of conception is, therefore, 0.33 MJ/kgW$^{0.73}$/day and the cost of pregnancy 0.151 MJ/kgW$^{0.75}$/day ([0.586 / 8.13] x 2.10).

Furthermore, using the latter figure, a recruitment curve can also be constructed to estimate the effects of *FpA* on the proportion of the females that give birth to young at the end of the gestation period. Here, it is assumed that if resource requirements are not met then the pregnancy is terminated. However, during gestation female wildebeest will have migrated from zone 3 to zone 1 and back again (Watson 1969; Talbot & Talbot 1963; Stuart & Stuart 1997; Kingdom 1997; Estes 1966; Delany & Happold 1979). Consequently, a pregnancy recruitment curve applicable to each zone is required (Appendix figure 1).

5.4.2 Survival of young

The third reproductive cost is lactation. Although a single representative value for the metabolic requirements of lactation has been given in section 5.4.1, this does not take into account growth of the young (Oftedal 1984; Theriez & Brelurut 1994). For instance, young reach nearly two-thirds of their adult weight within their first year (Talbot & Talbot 1963; Sinclair 1977b; Robbins & Robbins 1979; Figure 5.15). Consequently, their RMR increases, as do their demands for milk (Blaxter 1968, 1989). The amount of milk provided is dependent on two factors, the mother and the amount of resource available (Mduma *et al.* 1999). Sadleir (1969) states that in animals with prolonged periods of lactation, such as wildebeest, once a mother's requirements are satisfied, the remaining intake is converted directly into milk. The minimum amount of food a mother must consume for her young to survive is, therefore, equivalent to the combined metabolic requirements of both her and her young (Clutton-Brock *et al.* 1987a). Furthermore, during the lactating period, this minimum intake varies, not only because the energetic demands of young increase with growth (causing inter-seasonal variation; Mduma *et al.* 1999), but also because this period spans three different seasons in two different zones.

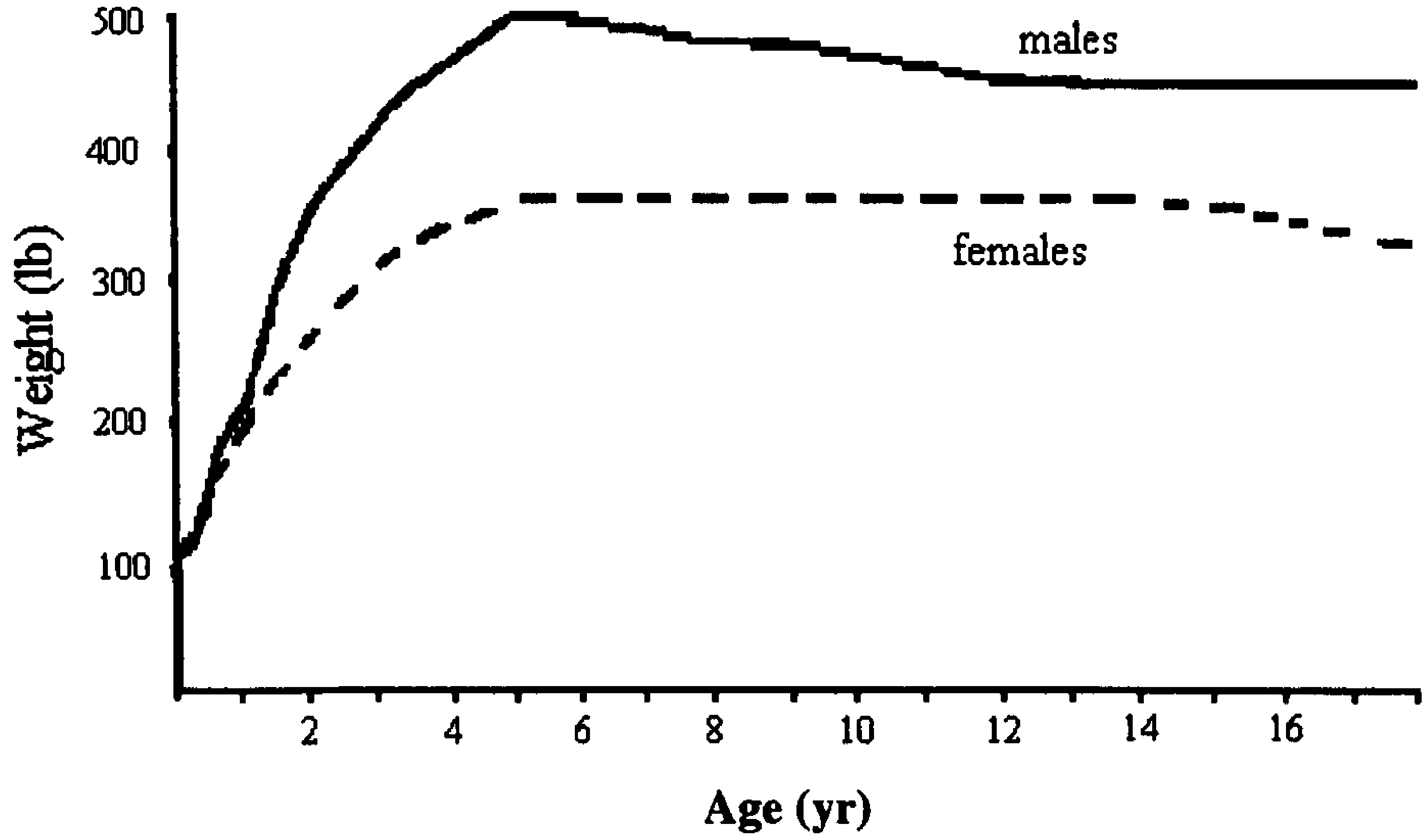

Figure 5.15 Average weights of wildebeest plotted against age (Talbot & Talbot 1963).

In order to incorporate all of this into the model, three survival curves are required. One representing the average weight range of young from birth to 4 months of age, occupying zone 3. Another for young between 4 and 9 months of age in zone 1 and a third curve for 9 to 12-month-old young, again in zone 3. To find the average weight range of young in each season, assuming that growth is constant (Talbot & Talbot 1963; Carles *et al.* 1981; Gerhart *et al.* 1994), the difference between the minimum weight at birth (14.5 kg) and the minimum weight at one year of age (116.7 kg; Talbot & Talbot 1963) is divided into twelve, monthly weights. The same is done for the maximum weights (25 kg to 134.5 kg), giving a monthly range (Table 5.7). An average, calculated from these ranges for each season, can be applied to a survival curve. Within these curves the RMR values estimated for each weight class are combined with equivalent maternal RMRs (section 5.3.2.2). As birth weight and growth rate of young are allometrically scaled to maternal weight, it was assumed that adult female RMRs in corresponding weight classes, previously used in the recruitment curves, would equate to the maternal RMRs (Robbins & Robbins 1979; Western 1979; Peters 1983;

Oftedal 1984; Clutton-Brock 1988). The minimum intake for each combined metabolic value is then calculated using the ME content of grass for the appropriate zone, from which a separate survival curve can be produced, thus incorporating both the growth of young and the seasonal availability of food (Appendix figure 2).

Table 5.7 Weight range from birth up to 1 year of age in wildebeest young.

		Weight range (kg)		Average weight range (kg)	
		Minimum	Maximum	Minimum	Maximum
Wet season	February (birth)	14.5	25.0	31.5	43.3
	March	23.0	34.1		
	April	31.5	43.3		
	May	40.1	52.4		
Dry season	June	48.6	61.5	69.7	84.3
	July	57.1	70.6		
	August	65.6	79.8		
	September	74.1	88.9		
	October	82.6	98.0		
Wet season	November	91.2	107.1	103.9	120.8
	December	99.7	116.3		
	January	108.2	125.4		
	February (1 year old)	116.7	134.5		

5.4.3 Reproductive strategy

As previously discussed, recruitment is a series of events resulting in the production of young capable of breeding (Blaxter 1989). The natural long-term objective of all individuals is to maximise recruitment, and hence, the intrinsic rate of natural increase of a population within a particular environment (Fraser 1968; Western 1979; Campbell 1996). This rate of increase is determined by the reproductive strategy adopted by that individual (Leuthold & Leuthold 1975; Estes 1976). It is made up of a number of variables, including litter size, frequency of reproduction, investment in parental care, and the duration, simultaneity, phenology (time of year) and synchrony (degree of co-ordination amongst a population) of reproductive events (Fraser 1968; Estes 1976; Western 1979; Campbell 1996; Sinclair *et al.* 2000).

Of course, many of these aspects have already been considered during the construction of the previous recruitment curves. What is has not been considered is that certain events may occur simultaneously. Wildebeest, for example, have the potential to give birth to one calf every year (Watson 1969). In order to achieve this, a female needs to be pregnant while feeding her current calf. Consequently, with a sufficient supply food, enough ME can be consumed to satisfy both processes concurrently and the intrinsic rate of natural increase will near its maximum. However, when food is limited, the ME consumed may only be enough to satisfy one of these processes. Given the amount of investment that has already gone into the existing offspring, it is assumed that a female's fertility or pregnancy will be suppressed (Verme 1962; Wiltbank *et al.* 1962, 1964, 1965; Smith 1964; McClure 1965; Wiltbank 1967; Clutton-Brock *et al.*1989). As a result, the intrinsic rate of natural increase may not only be considerably lower than the maximum, but population numbers maybe stunted as a result (Clutton-Brock *et al.* 1987b).

To incorporate the effect of *FpA* on population dynamics, a recruitment curve combining the metabolic costs of two concurrent reproductive processes is required. In wildebeest, there are four occurrences of simultaneous processes, each requiring a curve. The first is when females conceive while lactating. Consequently, the recruitment curve is based on a combination of the mother's RMR, conception costs and the RMR of a 0 to 4-month-old young. The other three cover the gestation period in which females can also have growing young (Appendix figure 3).

5.5 USING SURVIVAL AND RECRUITMENT TO PREDICT POPULATION NUMBERS

The next step is to determine the algorithms describing the relationship between *FpA* and the survival/recruitment within each curve. These algorithms can then be applied to the seasonal *FpA* figures predicted in the model, in order to estimate seasonal wildebeest numbers. The relationship between *FpA* and survival/recruitment is best described by a Richards' equation (Haefner 1996).

$$y = \frac{b_0}{(1 + (\frac{b_0}{b_1} - 1)e^{-b_2 b_3 x})^{\frac{1}{b_3}}} \tag{5.12}$$

The Richards' equation contains four coefficients. These are b_0, the maximal value of y, b_1, the value of y at $x = 0$, b_2 the slope of the curve and b_3 which scales the location of the inflection point along the x-axis. For the model, as survival can not exceed 100 %, $b_0 = 100$, and as each survival curve is symmetrical, the coefficient $b_3 = 1$ (Haefner 1996). This symmetry is a product of the linear relationship between weight and RMR, and the assumption that weight range is symmetrical about the mean of a normal distribution. This translates into an S-shaped logistic curve, although b_1 and b_2, still need to be determined. The coefficient b_1 was initially assumed to equal 0, as there is 0 % survival when *FpA* is 0. However, this results in a division by zero in equation 5.12 and therefore a positive value near to zero is required. In order to determine this value and that of b_2, a fitted curve was created to delineate each survival/recruitment curve in the model by iteratively adjusting the values for b_1 and b_2 until the coefficient of determination (R^2) was over 0.995 (considered to represent a satisfactory likeness). The values for these coefficients could then be applied to equation 5.12 and used in the model to estimate seasonal survival and recruitment.

5.5.1. Seasonal population numbers

The next step is to apply the seasonal *FpA* values to the appropriate equations, starting with those for the dry season in 1960. The resulting proportions can be used to estimate dry season survival and recruitment. For example, if 1,845,017 kg of green grass is available in zone 1 during the dry season of 1960 (1 kg/ha [grass available] x 1,845,017 ha [size of zone]), *FpA*, for 225,651 adult equivalents, is equal to 8.18 kg (see section 5.2.2). By applying this figure and the appropriate coefficients for adult survival to the Richards' equation (Equation 5.12), the proportion of adults surviving the dry season of 1960 is 0.958.

In other words, with 203,597 adults present at the beginning of the season (see section 5.2.1), 195,046 adults survive. This figure can be used to calculate the next season's survival figures and so on (see Figure 5.1). Similarly, seasonal juvenile survival can be estimated, as can recruitment. Furthermore, the cross-over of individuals into succeeding recruitment stages and functional groups can also be incorporated, as illustrated in figure 5.16 (refer also section 5.2.1).

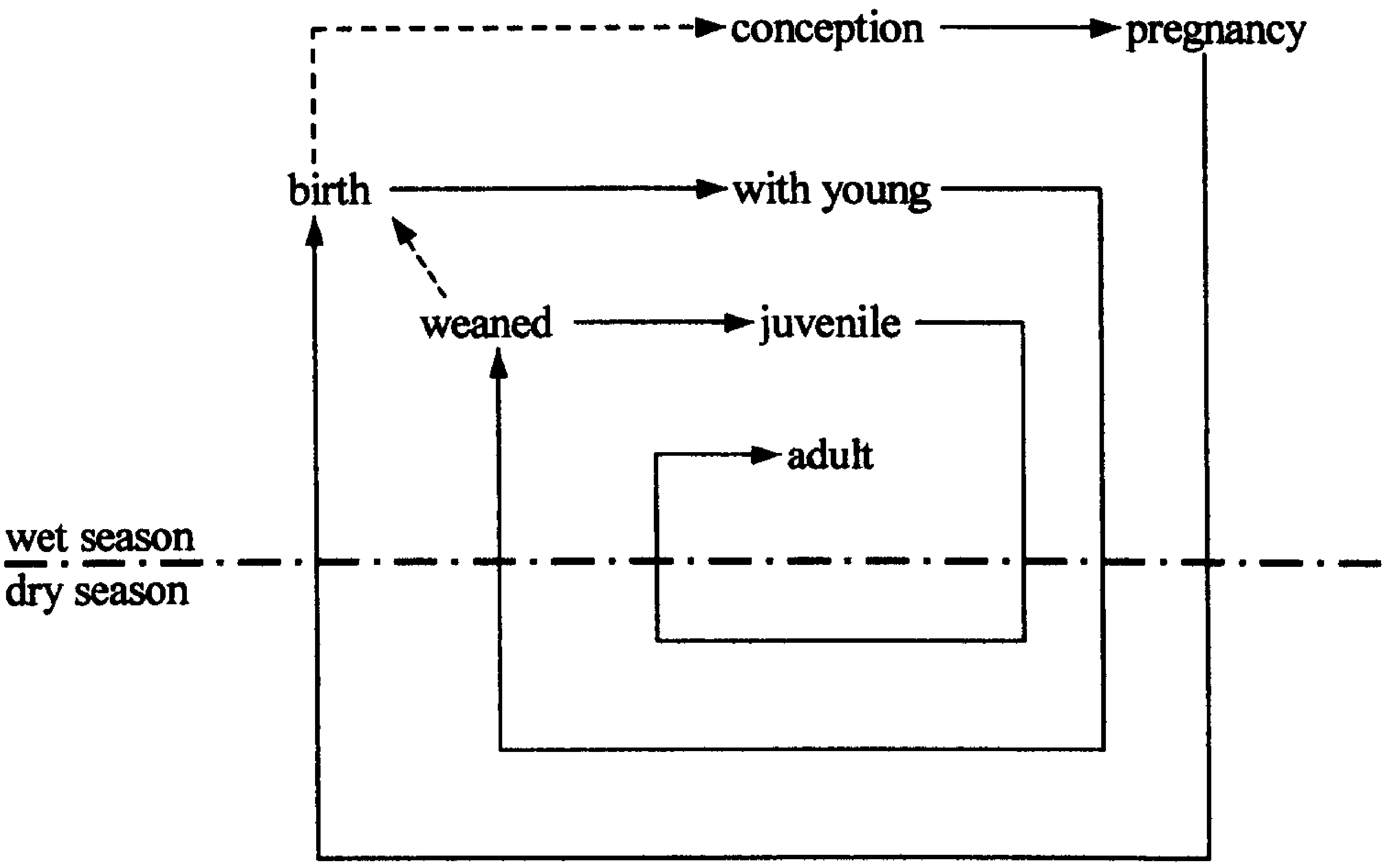

Figure 5.16 Recruitment cycle of wildebeest, the black lines indicate the process from conception to adult, while the dotted line indicates the divergence to the flow that allows female wildebeest to carry out two processes at the same time.

However, as females can conceive with and without young (indicated in Figure 5.16), an additional set of algorithms are required (Figure 5.17). At the beginning of each season, females can be in one of four possible categories; barren, pregnant, with young or pregnant with young (Clutton-Brock *et al.* 1989). By the end of a season, depending on *FpA*, a female's status may have changed. For instance, a terminated pregnancy leaves females barren or with young. The loss of both young and foetus again leaves females barren, and if other mortality factors are included in the model (see section 5.5.3), females can lose their young, but remain pregnant (Lamond 1970b). To account for these seasonal changes in status, the number of females in each category at the beginning of each season must be adjusted accordingly. In other words, if a female becomes barren having lost young, terminated her pregnancy or both, she will be included in the number of barren females at the beginning the next season.

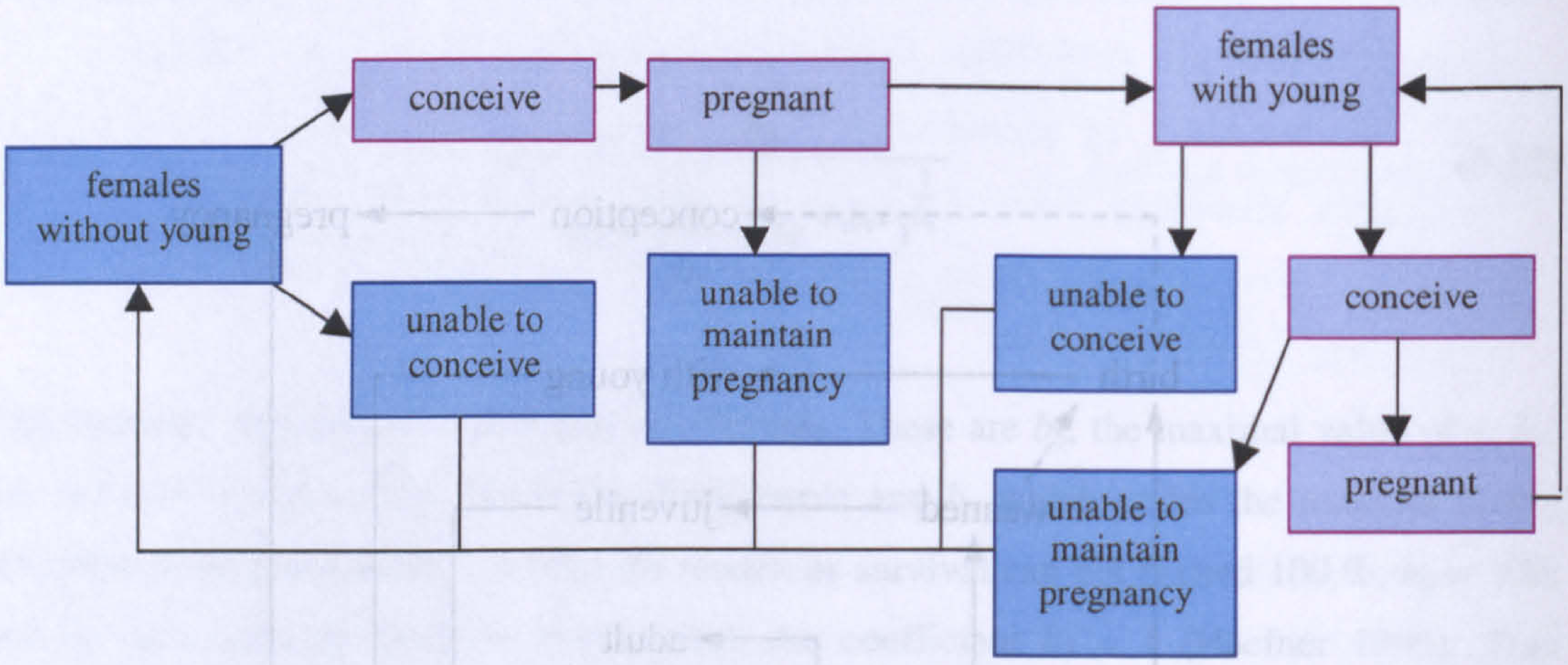

Figure 5.17 Flow chart to illustrate the various status of female wildebeest during to reproduction.

To initiate recruitment in the dry season of 1960, the number of females in each category is required. To determine these figures, the number of females within the adult wildebeest population and the number of young present during this time are a prerequisite. As previously estimated for the dry season of 1960, 102,000 females (section 5.4.1) and 37,000 young were present (see section 5.2.1). Mduma *et al.* (1999) state that in the wet season of 1959, pregnancy rate was 0.84. Assuming that no pregnancies were terminated before the start of the following dry season, the number of females pregnant was estimated to be 86,000 (102,000 x 0.84) and of these, 31,000 (37,000 x 0.84) have young as well. From such figures, it can be further estimated that 55,000 females are pregnant without young (86,000-31,000), 6,000 females are with young (37,000-31,000) and 16,000 females are barren (102,000-86,000).

5.5.2 Grass availability after grazing

As previously discussed in section 4.6, the amount of grass available is influenced by maturation, fire, and herbivory by insects, small mammals and large mammals (Sinclair 1975). To incorporate the latter into the model it was assumed that the amount of green grass available each week to wildebeest was dependent on the amount of grass growth and the amount of ungrazed, available green grass from the previous week. Of course, for there to be ungrazed green grass, there must be a limit to the amount an average wildebeest can consume (Prins & Olff 1998). Obviously, this is a physical constraint, as the rate of input to the mouth cannot exceed the output, (Illius & Gordon 1991, 1992; Belosky & Schmitz 1993; Gross *et al.* 1993b; Spalinger 1994; Prins & Olff 1998; Wilmhurst *et al.* 1999a). A simple way of estimating this maximum intake (I_{max}) value, is to assume that as reproductive strategies are the result of natural selection operating over evolutionary time under both environmental and physical constrains, the maximum rate of energy expenditure possible during recruitment is limited by the rate of energy acquisition (McNab 1980, Clutton-Brock 1988; Clutton-Brock *et al.* 1989). For wildebeest, the maximum energy expenditure occurs when females are pregnant while also feeding their 9-12 month old young. The *FpA* required by females to successfully do this, therefore, represents the maximum amount of food the average female wildebeest can consume in a day (i.e. 14.26 kg;). For the adult population, this daily intake value is 15.76 kg (14.26 kg/(average female weight [200 kg]) x (average adult weight [221 kg]). Consequently, the maximum amount of grass consumed in a particular zone and season is dependent on the total number of animals present. For example, in a week, the wildebeest population in the dry season of 1960 can consume is 24,893,818 kg ([15.76 x 7] x 225,651 (the number of adult equivalents)). Where weekly food availability in zone 1 exceeds this maximum intake value, the excess is carried forward the next week's availability. Where food availability is lower, all the grass is assumed to be grazed, and nothing is carried forward. By incorporating this into the model, the average weekly amount of grass available each season, from which seasonal *FpA* is calculated and subsequent population dynamics is based, will reflect the take-off by grazing.

5.5.3 Outcome

Although seasonal population numbers of wildebeest can now be estimated, the model must also account for two factors that significantly affect population dynamics; non-food-related mortality and competition. Of course, there are many different causes of mortality, including disease and predation (Sinclair 1974d; McNaughton & Georgiadis 1986; Mills *et al.* 1995). The application of mortality through disease is not straightforward, as disease-related mortality is generally dependent on an animal's nutritional status (Borner *et al.* 2000). For instance, for ecto- and endoparasites to reach fatal numbers, an animal must have inadequate disease resistance, which tends to occur when it is undernourished (Talbot & Talbot 1963; Hillman & Hillman 1977; Borner *et al.* 2000). This is, therefore, a secondary cause of mortality, which simply accelerates death (Sinclair 1974d). Consequently, only nutritionally independent diseases cause additional mortality. However, no endemic diseases or epidemics have been documented in the Serengeti-Mara ecosystem following the removal rinderpest (section 2.3.2; Prins & Weyerhaeuser 1987). As a result, this type of disease-related mortality cannot be incorporated into the model. Mortality through predation, however, will be dealt with in chapter 7, while the following chapter outlines the addition of other herbivores into the model to incorporate the effects of inter-specific competition for the same resource.

CHAPTER 6: HERBIVORE COMPETITION

6.1 INTRODUCTION

It is believed by many, although there is little evidence, that the long-term effects of interspecific competition are in part responsible for shaping ecological communities, such as the Serengeti-Mara ecosystem (Pereira 1961; Lamprey 1963, Talbot 1966; Field 1968b; Connell 1983; Salt 1984; Strong *et al.* 1984; Sinclair 1985; Keddy 2001). The continuing pressures that this process exerts on different species within an ecosystem has led to resource partitioning and niche separation, which in turn has enabled many species to coexistence (Lamprey 1963; Hurlbert 1978; Jarman & Sinclair 1979; Sinclair 1979a; Jackson 1981; Hansen *et al.* 1985; Murray & Illius 2000; Keddy 2001). However, this occurs over a large time-scale and only the regulating effects of interspecific competition, on annual herbivore population dynamics within the time period of the model, are being considered (Sinclair 1974a, d). This chapter concentrates on interspecific competition for food, and its role in the population dynamics of various herbivore components within the Serengeti.

Here, the level of competition for grass occurring amongst grazing herbivores is primarily influenced by the amount of food available per animal (*FpA*) (Sinclair 1974d; Walker *et al.* 1981; McNaughton & Georgiadis 1986; Fryxell *et al.* 1988; de Boer & Prins 1990; Illius & Gordon 1992; Prins & Olff 1998; Ottichilo *et al.* 2001). For example, in zone 1 during the dry season, available grass is fed upon by both migratory and resident grazing herbivores (Borner *et al.* 1987; Fryxell *et al.* 1988). However, during the wet season only resident herbivores utilise this resource. Therefore, *FpA* varies in relation to grass growth during the wet season and to the total number of individuals exploiting it at this time (Noy-Meir 1982; Borner *et al.* 1987; Boutton *et al.* 1988b; de Boer & Prins 1990). Subsequently, when the amount of food available does not satisfy the requirements of all the animals feeding upon it, mortality rates increase and/or reproductive rates decrease (Prins & Olff 1998). It is this density dependent process that is considered to be a principal regulator of population dynamics (Sinclair 1974a, d; Chesson & Rosenzweig 1991; Prins & Olff 1998).

In order to include this in the model, a further ten grazing herbivore components are incorporated into the six sub-models. The total number of grazing individuals in each zone and season can then be used to estimate specific *FpA* for each component. The predicted seasonal survival of each, based on these figures, will reflect both the intraspecific and interspecific food competition. This assumes that the amount of grass available is equally distributed within each zone and equally accessible to all grazing herbivores within that specific region (Kreulen 1975; Jarman & Sinclair 1979; Noy-Meir 1982; Owen-Smith & Novellie 1982; Sinclair 1985; de Boer & Prins 1990; Chesson & Rosenzweig 1991). Furthermore, there is no transfer of grazing individuals between zones unless otherwise stated (i.e. with migrants) and, as previously mentioned, there are no selective preferences for specific grass species, parts or morphs, again unless otherwise stated (Vesey-Fitzgerald 1960; Talbot & Talbot 1962; Field 1968a, c; Gwynne & Bell 1968; Bell 1969). Further discussion on how each component's population numbers are regulated by this competition appears in chapter 8.

6.2 ADDING OTHER GRAZING HERBIVORES INTO THE MODEL

The same procedure used to predict seasonal population numbers for wildebeest in chapter 5 was used to predict those of each of the other grazing herbivore components to be added to the model (see section 2.3.1). Of course, the recruitment processes and reproductive strategies adopted by these herbivores are variable (e.g. gestation period, annual birth seasons, timing of births, age at sexual maturity and time of weaning) and these variations can influence the intrinsic rate of natural increase, which is subsequently reflected in their seasonal population numbers (Fraser 1968; Leuthold & Leuthold 1975; Estes 1976; Western 1979; Campbell 1996; Sinclair *et al.* 2000).

Consequently, each component needs a set of survival curves that are applicable to its reproductive cycle and functional groups. Moreover, these need to represent the zones occupied by each of the components, as the metabolic energy (ME) they receive per kilogram of grass varies depending on the zone they inhabit. The following sections outline each herbivore component added to the model and discusses any modifications made to the original method used for wildebeest (given in chapter 5).

6.2.1 Buffalo

Buffalo are predominantly grazers, preferring to inhabit the wooded grasslands of zones 1 and 2 (Dorst & Dandelot 1970; Briand Petersen & Casebeer 1971; Sinclair 1973, 1974a, 1977b; Delany & Happold 1979; Hansen *et al.* 1985; Estes 1991; Kingdon 1997; Stuart & Stuart 1997). They are considered to be the closest competitor of wildebeest, although this appears only to come into effect when migrant animals move into the same zones during the dry season (Lamprey 1963; Gwynne & Bell 1968; Sinclair & Gwynne 1972; Sinclair 1974a, d; de Boer & Prins 1990). As green grass growth is at its minimum at this time, migratory wildebeest, zebra and Thomson's gazelle arrive in zones 1 and 2 when the pressures of competition will be at their greatest (Sinclair & Gwynne 1972). It has been proposed that it is this heightened competition at a time when grass is a limiting factor, both in terms of quantity and quality, that regulates annual population numbers of migratory and resident components (Sinclair *et al.* 1985; Fryxell *et al.* 1988). This issue will be investigated further in the present model (see chapter 8), once the following herbivore components have been included.

Buffalo are incorporated into the model in much the same way as wildebeest, as their recruitment process and reproductive strategy are fairly similar (see section 5.5.1). Like wildebeest, buffalo are capable of producing one calf a year and the majority of young are born within a month of each other (Sinclair 1974b, 1977b; Grimsdell 1973; Estes 1991; Stuart & Stuart 1997). Such pronounced birth peaks have been identified in all of the grazing herbivore components, even though each can produce young all year round (Kayanja 1969; Spinage 1972; Anderson 1975; Dunham & Murray 1982; Estes 1991; Walther 1995; Stuart & Stuart 1997; Sinclair *et al.* 2000). Investigations have shown that these peaks occur when the majority of females synchronise the reproductive process, requiring the greatest energetic intake, with maximum food availability (Sinclair 1974b; Kiltie 1984). This is particularly convenient for the present model, as it is much simpler to assume, as it has been for wildebeest, that all young are born during these peaks. For example, all buffalo are born in April during the wet season (Sinclair 1974b; 1977b; Grimsdell 1973; Estes 1991; Stuart & Stuart 1997).

There are, however, a few differences between wildebeest and buffalo that require the latter's survival/recruitment curves and set-up within the model to be adjusted. The first is that as buffalo are one of the largest grazing bovids (males range in weight from 410 kg to 870 kg and females range from 350 kg to 600 kg; Robinette 1963, Sachs 1967; Ledger 1963; Kingdon 1982a, 1997; Estes 1991), each life history stage takes longer in comparison to other bovids (Fraser 1968; Blueweiss *et al.* 1978; Western 1979). In particular, females, on average, do not reach sexual maturity until they are forty-eight months of age (Briand Petersen & Casebeer 1971; Sinclair 1974b, 197b7; Grimsdell 1973; Estes 1991). Therefore, the juvenile functional group spans three years (from the 12th month to the 48th month), during which time growth continues (Markus 1943; Prins 1989). The difference in weight between juveniles from one year to the next will therefore influence their survival. Consequently, a survival curve was constructed for each juvenile year. The average weight ranges used for each were estimated from birth weight data (35 to 55kg; Markus 1943; Vidler *et al.* 1963; Sinclair 1974b, 1977b; Estes 1991; Stuart & Stuart 1997), and the adult weight range (350 kg to 870 kg). By taking into account that buffaloes reach full development by their 5th year, and assuming that growth is constant, appropriate weight ranges were calculated (Markus 1943; Prins 1989). For juveniles between 12 and 24 months of age, the average weight range was estimated to be 129.5 kg to 299.5 kg. For 24 to 36 month-old juveniles, the range was 192.5 kg to 462.5 kg, and finally for 36 to 48 month juveniles, the range was estimated at 255.5 kg to 625.5 kg. Furthermore, the method used in the model to predict seasonal juvenile numbers was adjusted to accommodate these two additional juvenile years. Figure 6.1 illustrates the buffalo recruitment process.

One further source of variation, according to Blaxter (1989), is that the crude energetic costs of conception, pregnancy and lactation vary between those species that are taxonomically similar to a sheep, like the wildebeest, and those that are similar to a cow, such as the buffalo (Brashares *et al.* 2000). Using the daily cost of lactation for a cow (0.278 MJ/kg $W^{0.75}$) given by Blaxter (1989), to represent buffalo, the cost of conception (0.161 MJ/kg$W^{0.73}$/day) and pregnancy (0.072 MJ/kg $W^{0.75}$/day) were estimated (see section 5.4.1). These were applied appropriately to the buffalo recruitment curves, which in turn, were applied to the model in order to calculate apropos seasonal population numbers.

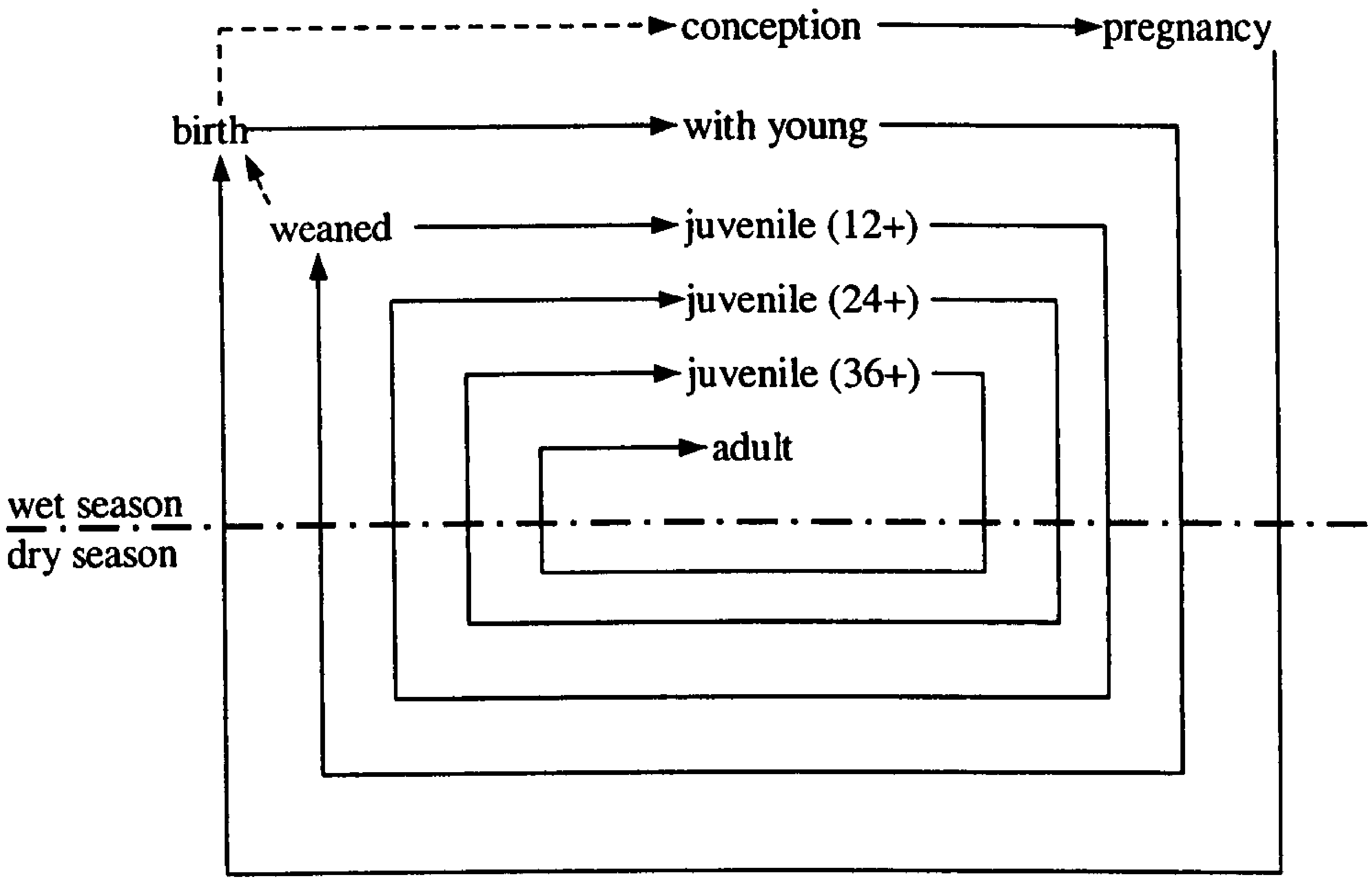

Figure 6.1 Recruitment cycle of buffalo. Black lines indicate the process from conception to adult, while the dotted line indicates the parallel flow that allows female buffalo to carry out two processes simultaneously, age in months in brackets, and finally the dot-dashed line separates the dry and wet season (Vidler *et al.* 1963; Grimsdell 1969, 1973; Dorst & Dandelot 1970; Sinclair 1974b, 1977b; Modha & Field 1974; Field 1976; Kingdon 1982a, 1997; Estes 1991; Stuart & Stuart 1997; Sinclair *et al.* 2000).

6.2.2 Migratory zebra

There is the potential for a high level of competition between migratory zebra and wildebeest. Not only are they both exclusively grazers, but they follow a very similar migratory pattern, exploiting the same zones in the same seasons (see selection 3.3.5; Stewart & Stewart 1970; Owaga 1975; Hansen *et al.* 1985; de Boer & Prins 1990). However, one fundamental difference is diet selection. Owaga (1975) found that the proportion of green grass in a zebra's diet corresponded to availability and concluded that they were relatively non-selective feeders (see section 4.5). Their physiology enables them to utilise grass that is nutritionally poor in quality, compensating for lower metabolic energy (ME) content by increasing food intake and gut passage rates (Delany & Happold 1979; Crawley 1983, Beekman & Prins 1989; Twine 2002). Zebra survival and recruitment, therefore, depends on the total amount of grass available (dry and green) and the overall ME content of that grass. Consequently, in order to construct representative survival and recruitment curves for zebra, the amount of grass required to satisfy their metabolic demands must be calculated using the appropriate ME content in their diet. However, this value fluctuates depending on the proportion of green to dry grass in a particular season. It was considered that four scenarios, and therefore four sets of survival/recruitment curves, could be effectively used to represent these fluctuations on a relatively simple scale. The first is where green grass constitutes 75 % to 100 % of the total amount of grass present, the second constitutes 50 % to 75 %, the third constitutes 25 % to 50 % and the last is where 0 % to 25 % of green grass is present.

In order to estimate the average ME content per kilogram of grass for each of these scenarios, the average ME content of dry grass is required. As grass is considered to be mature when crude protein levels drop to 0.04 kg/kg grass, this is assumed to be the maximum crude protein value of dry grass. The minimum is taken to be an average of measurements made by Sinclair (1985) and Duncan (1975), who found that the minimum crude protein (*CP*) content of dry grass was 0.024 kg/kg grass (2.8 % & 2 % respectively). It was assumed that taking an intermediate of these two extremes would adequately represent the average *CP* content of dry grass, therefore 0.032 kg/kg grass. Equations 5.7 and 5.8, given by Murray (1991), were used to calculate the ME content of dry grass (see section 5.3.2.1). This was estimated to be 6.98 MJ/kg. By combining this value with the average ME content of green grass, for zones 1, 2 and 3 (8.89 MJ/kg grass, 8.89 MJ/kg grass and 9.13 MJ/kg grass respectively, see section 5.3.2.1), the average ME content of grass for each of the scenarios was calculated (Table 6.1).

Table 6.1 Estimated metabolic energy content of grass in each zone, when the proportion of green grass to dry grass is between 100 and 75 %, 75 and 50 %, 50 and 25 %, and 25 and 0 %.

Scenario (Percentage of green grass to dry grass)	ME content of grass (MJ/kg grass) in zones 1 & 2	ME content of grass (MJ/kg grass) in zone 3
100 - 75 %	8.65	8.86
75 - 50 %	8.17	8.32
50 - 25 %	7.70	7.79
25 - 0 %	7.25	7.22

There are three further differences between zebra and wildebeest that could influence population numbers. The first is that the crude energetic costs of conception, pregnancy and lactation vary for species that are taxonomically similar to a horse (Blaxter 1989; Brashares *et al.* 2000). By assuming that the daily cost of lactation for a horse (0.344 MJ/kgW$^{0.75}$) given by Blaxter (1989) represents zebra, the cost of conception (0.199 MJ/kgW$^{0.73}$/day) and pregnancy (0.089 MJ/kgW$^{0.75}$/day) were estimated and applied appropriately to recruitment curves (see section 5.4.1).

The second possible source of variation is that the relationship between body weight and RMR may be different for species within the order Perissodactyla compared to those in the order Artiodactyla. However, although Hayssen & Lacy (1985) investigated this relationship for many taxonomic groups (see section 5.3.1), they were unable to do so for Perissodactyla as they only found raw data for one equine species. This was taken from Yousef & Dill (1969), who measured the BMR for an individual ***Equus asinus*** weighing 177.5 kg, to be 0.165 ml O_2/g-hr. Converting this value into an RMR equivalent, gives a figure of 42.4 MJ/day (see section 5.3.1). If this is compared to the equivalent RMR for an Artiodactyla of the same weight, that is 58.4 MJ/day, it would appear that RMRs for the order Perissodactyla are lower. However, in a diagram produced by Blaxter (1989) to illustrate the relation between the rate of minimal metabolism and body weight of species in different taxonomic groups, Perissodactyla have marginally higher MMRs than Artiodactyla of the same weight (Figure 6.2). As a result of this conflicting information, it could only be assumed for the purposes of the model that the relationship between body weight and RMR for Artiodactyla and Perissodactyla was the same.

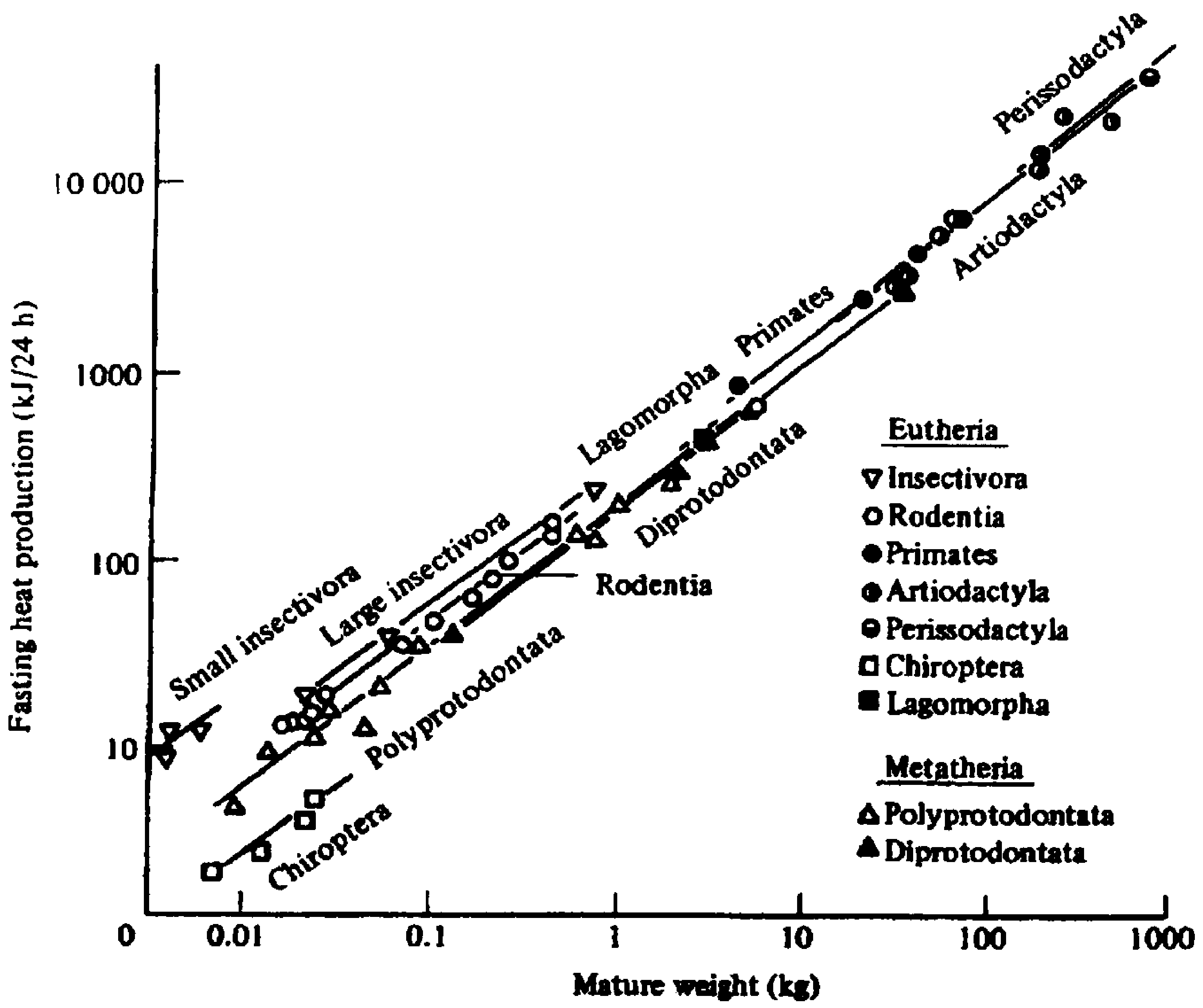

Figure 6.2 The relation between minimum metabolic rates and body weight on species for different taxonomic groups (Blaxter 1989).

Zebra life history also varies in comparison to wildebeest. For instance, young are weaned six months earlier, but sexual maturity is not reached until a year after that of wildebeest (Figure 6.3; King 1965; Klingel 1965, 1969; Carter 1984; Kingdom 1997; Asa 2002). Hence, the juvenile functional group includes individuals between 6 months and 24 months of age. Consequently, a juvenile survival curve encapsulating a year, as used for both wildebeest and buffalo, could not be applied to zebra, especially as a large proportion of their total growth occurs during this time (King 1965). Taking this into account, seasonal survival curves were constructed instead. Monthly growth rates were calculated, as for buffalo, from birth weight data (30 to 35 kg; King 1965; Stuart & Stuart 1997) and the adult weight range (175 to 250 kg for females and 220 to 340 kg for males; Sachs 1967; Dorst & Dandelot 1970; Kingdom 1997; Stuart & Stuart 1997). These were then used to estimate the average weight ranges of juveniles within each of the seasons this functional group spans. Four survival curves were therefore constructed, one for 6 to 9 month old juveniles in their first dry season (75 to 130 kg), one for 9 to 16 month-old juveniles in the following wet season (106 to 194 kg), another for 16 to 21 month-old juveniles in the second dry season (142 to 270 kg) and finally, one for 21 to 24 month-olds in the wet season in which they become adults (166 to 321 kg).

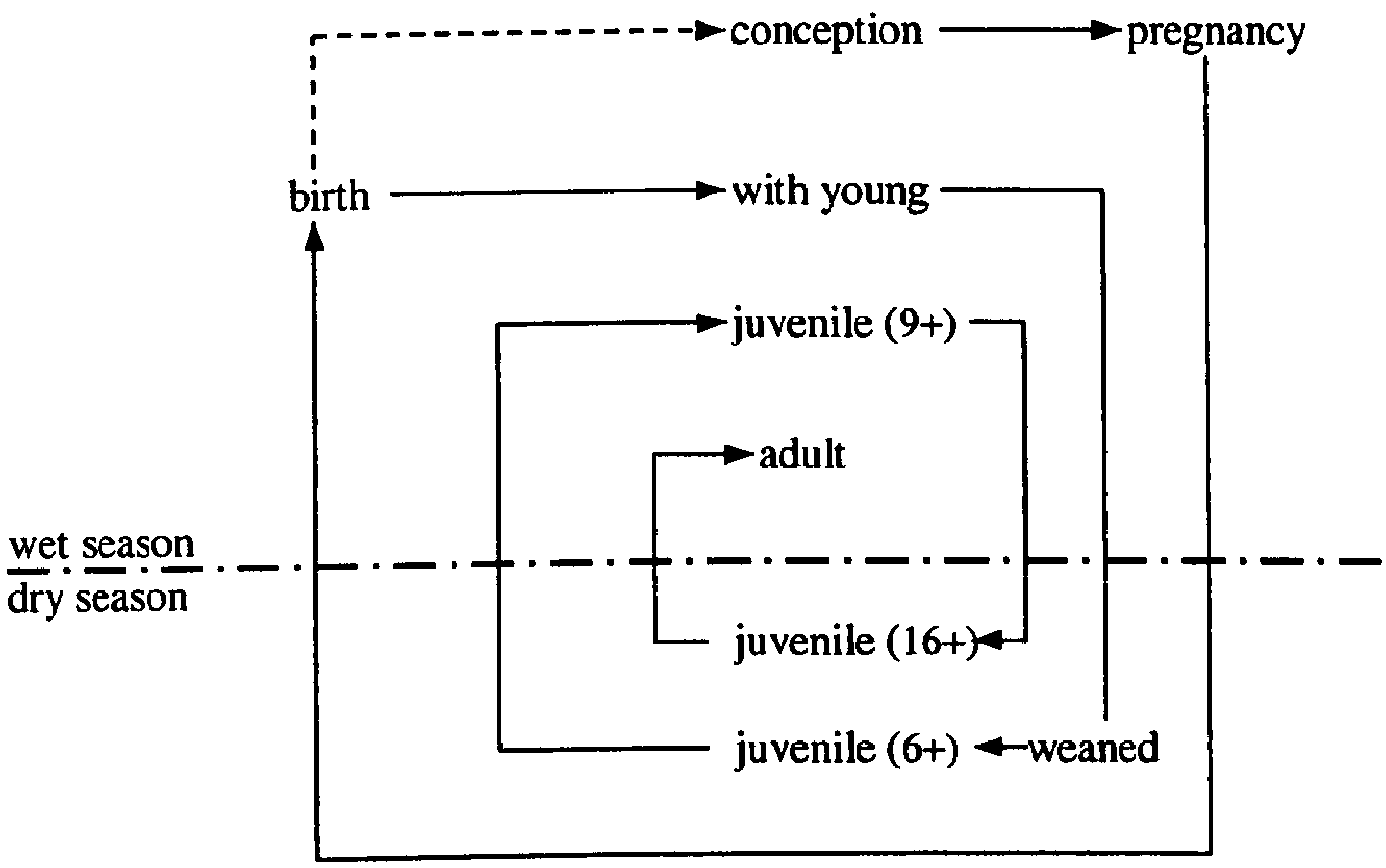

Figure 6.3 Recruitment cycle of migratory zebra. Black lines indicate the process from conception to adult, while the dotted line indicates the parallel flow that allows females to carry out two processes simultaneously. Age in months is shown in brackets and the dot-dashed line separates the dry and wet season (King 1965; Klingel 1965, 1969; Dorst & Dandelot 1970; Leuthold & Leuthold 1975; Delany & Happold 1979; Carter 1984; Estes 1991; Kingdom 1997; Stuart & Stuart 1997; Sinclair *et al.* 2000; Asa 2002; Saltz 2002).

6.2.3 Migratory Thomson's gazelle

Similar to the other migratory components, Thomson's gazelle are essentially grazers (Lamprey 1963; Maloiy 1963; Stewart & Stewart 1970; Hansen *et al.* 1985). Although investigations have revealed that during the dry season, browse can constitute up to 10 % of their diet, this was not considered in the model (Talbot & Talbot 1962; Gwynne & Bell 1968; Bell 1969; Kingdon 1982b).

As one of the smallest bovids (ranging from 12.1 to 23.5 kg in females and 17 to 29.1 kg in males; Ledger 1963; Sachs 1967; Estes 1991; Kingdon 1982b, 1997; Stuart & Stuart 1997), the Thomson's gazelle's life history stages occur over a relatively short period of time (Fraser 1968; Western 1979). For instance, young are weaned within two months of birth, and females are sexually active after only a year (Hvidbeg-Hansen 1970; Robinette & Archer 1971; Delany & Happold 1979; Kingdon 1982b; Furley 1986;

Parker 1990; Nowak 1995; FitzGibbon 1994; Walther 1995). Furthermore, as gestation only lasts approximately six months, under favourable conditions females can produce young twice a year, with one birth peak in January and another in July (Brooks 1961; Estes 1967, 1991; Hvidbeg-Hansen 1970; Robinette & Archer 1971; Leuthold 1972; Delany & Happold 1979; Western 1979; Kingdon 1982b; Georgiadis 1985; Furley 1986; Parker 1990; Nowak 1995; FitzGibbon 1994; Stuart & Stuart 1997). Figure 6.4 illustrates the recruitment process of Thomson's gazelle.

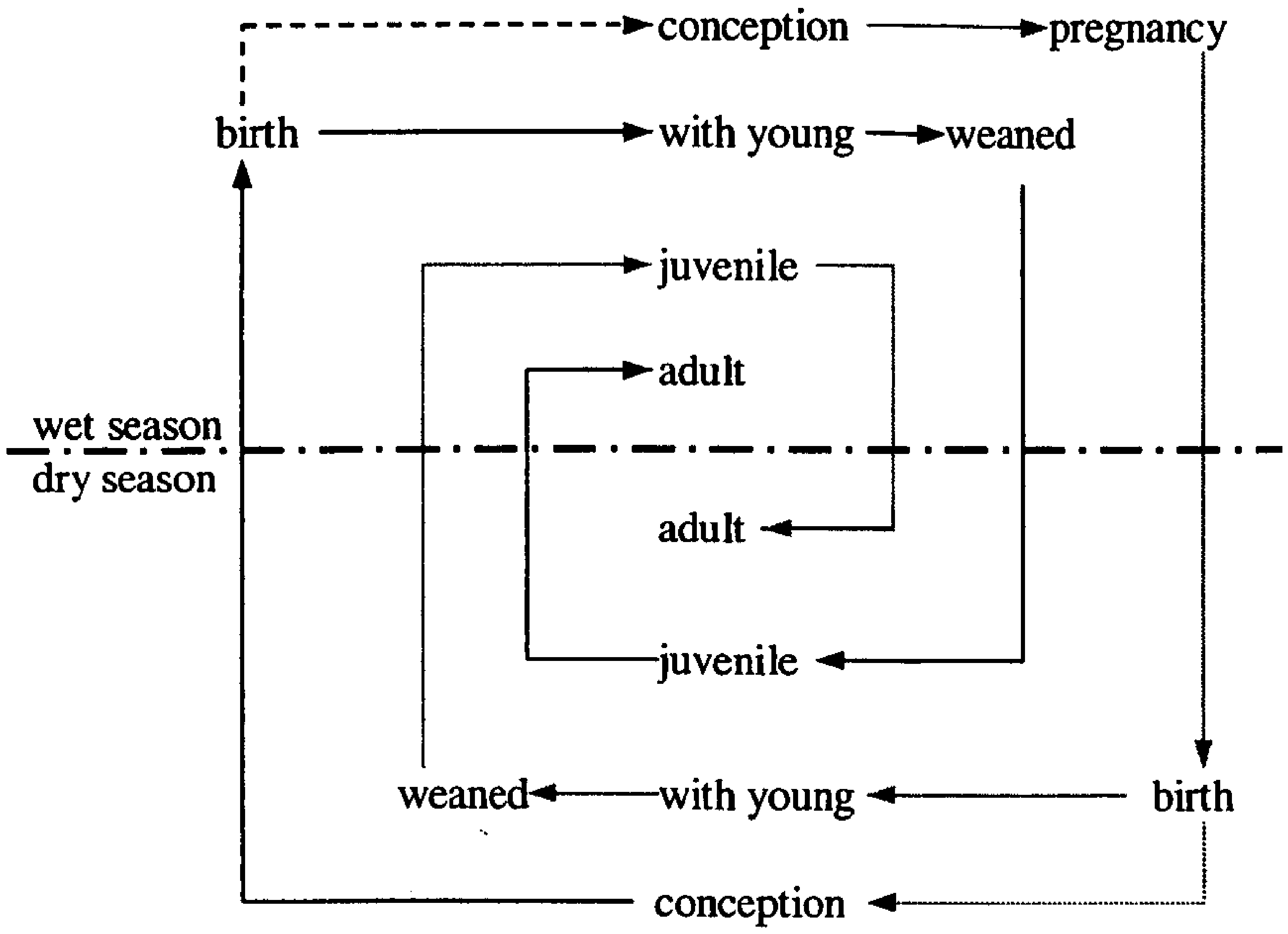

Figure 6.4 Recruitment cycle of migratory Thomson's gazelle. Dotted line indicates the parallel flow that allows females to carry out two processes simultaneously, black lines indicate the process from conception to adult of young born in the January birth peak and grey lines follow the process for young born in July. The dot-dashed line separates the dry and wet season (Brooks 1961; Estes 1967, 1991; Hvidbeg-Hansen 1970; Robinette & Archer 1971; Leuthold 1972; Delany & Happold 1979; Western 1979; Kingdon 1982b; Georgiadis 1985; Furley 1986; Parker 1990; Nowak 1995; FitzGibbon 1994; Walther 1995; Stuart & Stuart 1997).

As for migratory zebra, survival rates for juvenile Thomson's gazelle were estimated on a seasonal basis. However, as the average weight range varies between those juveniles born in the wet season and those born in the dry, a set of survival curves was essentially made for both. For individuals born in the January birth peak in the wet season, survival curves were constructed for juveniles between 2 and 5 months of age (4.1 to 8.1 kg), 5 and 10 months of age (6.3 to 13.9 kg) and 10 and 12 months (8.3 to 19 kg). Alternatively, individuals born in the July birth peak in the dry season, required survival curves for 2 to 4 month-old juveniles (3.9 to 7.4 kg), 4 to 11 month-olds (6.3 to 13.9 kg) and 11 to 12 month-old juveniles (8.5 to 19.7 kg). Again, their ranges were estimated using birth weight data (2.2 to 3 kg; Kingdon 1982b, Georgiadis 1985; Stuart & Stuart 1997) and the adult weight range that is reached by 18 months of age (Delany & Happold 1979).

6.2.4 Grant's Gazelle

As Grant's gazelle and Thomson's gazelle belong to the same genus, it is not surprising that they have a very similar biannual reproductive strategy (Figure 6.5; Owen-Smith 1977; Estes 1991; Walther 1995; Kingdon 1997; Stuart & Stuart 1997; Sinclair *et al.* 2000). However, as Grant's are somewhat larger (35 to 67 kg for females and 53 to 81 kg males; Sachs 1967; Kingdon 1982b, 1997; Estes 1991; Stuart & Stuart 1997), some of their reproductive stages tend to take longer (Fraser 1968; Western 1979). For instance, weaning occurs at 6 months and sexual maturity occurs at 18 months of age (Kingdon 1982b, 1997; Furley 1986; Estes 1991). Consequently, survival rates were estimated for juveniles born in the wet season between 6 and 10 months of age (13.1 to 29.2 kg), 10 and 17 months (20.7 to 47.2 kg) and from 17 to 18 months of age (20.1 to 60.2 kg). For individuals born in the dry season, survival curves were constructed for 6 to 11 month old juveniles (13.8 to 30.8 kg), 11 to 16 month olds (20.7 to 47.2 kg) and for 16 to 18 month olds (25.4 to 58.6 kg). The birth weight range of 5 to 7 kg (Georgiadis 1985; Stuart & Stuart 1997) and the adult weight range attained at the age of 24 months, were used to estimate the average weight ranges within each juvenile survival curve (Delany & Happold 1979).

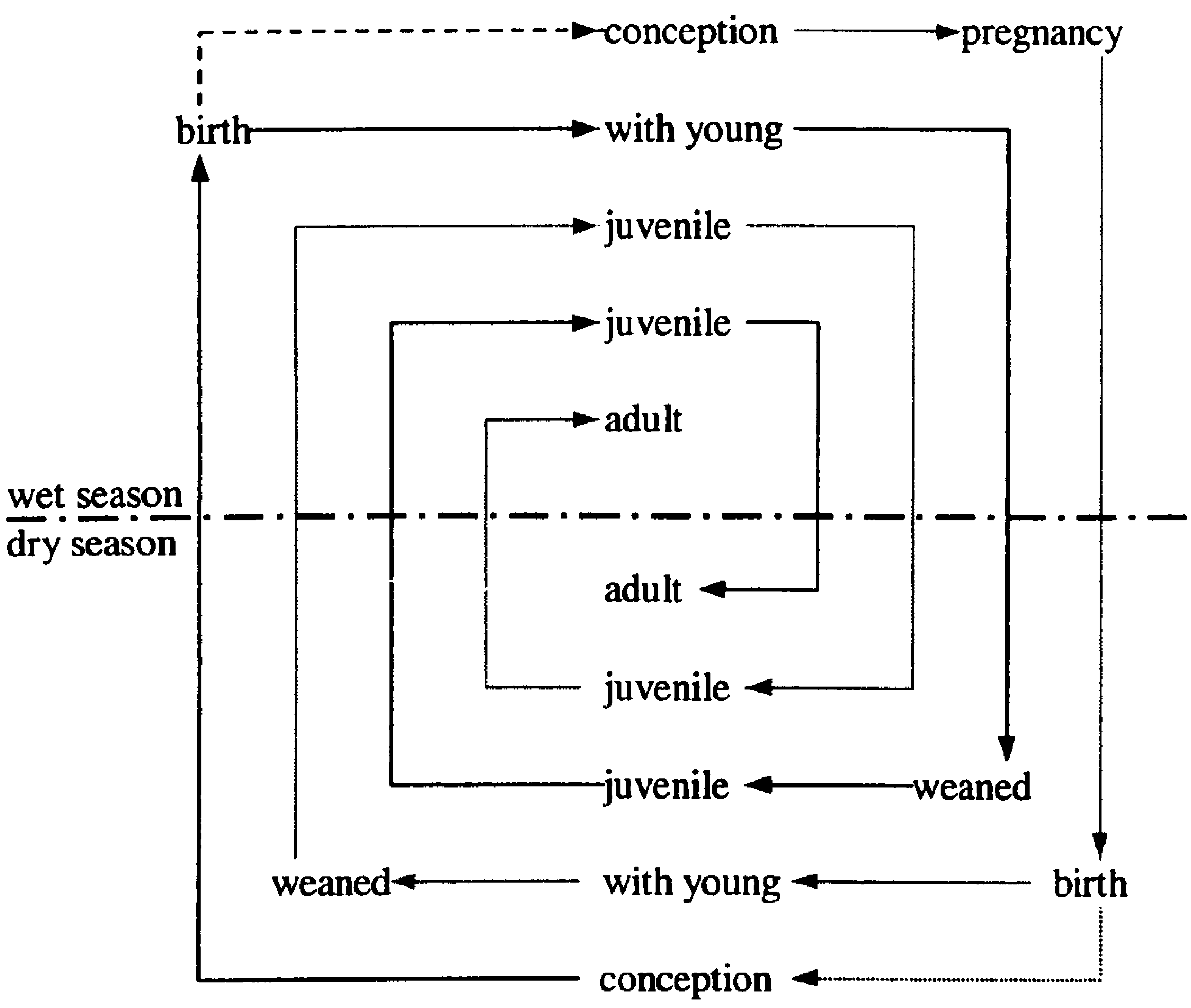

Figure 6.5 Recruitment cycle of Grant's gazelle. The dotted line indicates the parallel flow that allows females to carry out two processes simultaneously. Black lines indicate the process, from conception to adult, of young born in the wet season birth peak. Grey lines follow the same process for young born in dry season and the dot-dashed line separates the dry and wet season (Leuthold 1972; Western 1979; Kingdon 1982b, 1997; Furley 1986; Estes 1991; Walther 1995; Stuart & Stuart 1997; Sinclair *et al.* 2000).

One fundamental difference between the two gazelle species is that although Thomson's gazelle occasionally browse in the dry season, this type of foliage constitutes a major part of the Grant's gazelle's diet. As a consequence, they have been categorised as mixed feeders (Talbot & Talbot 1962; Lamprey 1963; Maloiy 1963; Stewart & Stewart 1970; Underwood 1981; Hansen *et al.* 1985; Stuart & Stuart 1997). Studies investigating Grant's gazelles' diet preference have revealed that they tend to switch from being a pure browser to being a pure grazer when flushes of green grass are brought on by rainfall (Spinage *et al.* 1980). As a result, during the wet season when green grass is more abundant, Grant's gazelle tend to graze and during the majority of the dry season they appear to browse (Estes 1991, Hofmann 1973, Spinage *et al.* 1980; Kingdon 1982b, 1997, Dorst & Dandelot 1970). At this point in the construction of the model, the detailed dynamics of the plant species that provide browse is not being considered. Therefore, the survival of Grant's gazelle during the dry season is assumed, for the purposes of this model, to be the same as if they were eating green grass. Using survival/recruitment curves for the green grass and estimating an equivalent *FpA* for each dry season, crude population numbers were calculated. Grant's gazelle, however, did not contribute competitively with the other grazing herbivores at this time, nor did they influence the amount of green grass available. Of course, the only way to determine whether these figures appropriately reflect the survival of browsing gazelles is to compare them with actual annual population numbers and this will be reviewed in chapter 8.

6.2.5 Impala

This Aepycerotini is of a similar size to Grant's gazelle (38.9 to 60 kg for females and 45 to 80 kg for males; Sachs 1967; Kingdom 1982b, 1997; Estes 1991), but its slightly longer gestation period of 7 months prevents females from having two births a year (Kayanja 1969; Kingdon 1982b; Georgiadis 1985; Stuart & Stuart 1997). Instead, the majority of females do not conceive directly after birth, but five months later (Jarman & Jarman 1974; Kingdon 1982b). There are two possible reasons for this. The first is that there may be a selective advantage in synchronising birth with the onset of the wet season (Warren 1974; Kingdon 1982b). Secondly, during the breeding period males enter what is known as the rut. This is when males defend patches of land which are likely to be visited by females (Gosling & Petrie 1990). The more favourable a particular area is to females, the more matings the male occupier of that area will have. Consequently, there is intense competition for areas that attract the most females (Jarman & Jarman 1973). Furthermore, once a male has established an area, he must continually defend it, and the females that enter it, from other males, as well as mating with as many females as possible (Jarman & Jarman 1973; Kingdon 1982b). This practice incurs high energetic costs and males can die from exhaustion during this period (Gosling *et al.* 1987). In order for males to survive this period and successfully mate, they must first be in peak physical condition. In fact, studies have shown that male impala are incapable of breeding until they have reached this high level of condition, which may explain why the rut does not occur until the fifth month of the wet season (Skinner 1971; Fairall 1972; Skinner *et al.* 1974, Kingdon 1982b).

Like Grant's gazelle, female impala reach sexual maturity at 18 months, which coincides with the rut. As a result there are two survival curves for the juvenile functional group, one for juveniles aged between 7 and 12 months (16.7 to 33.5 kg) and the other for 12 to 18 month-olds (25.9 to 52.7 kg). These weight ranges are again estimated from birth weight data (4 to 6 kg; Georgiadis 1985; Stuart & Stuart 1997) and from the adult weight range attained at 24 months of age (Delany & Happold 1979; Kingdon 1982b; Estes 1991). Figure 6.6 illustrates the relatively simple reproduction cycle employed by impala.

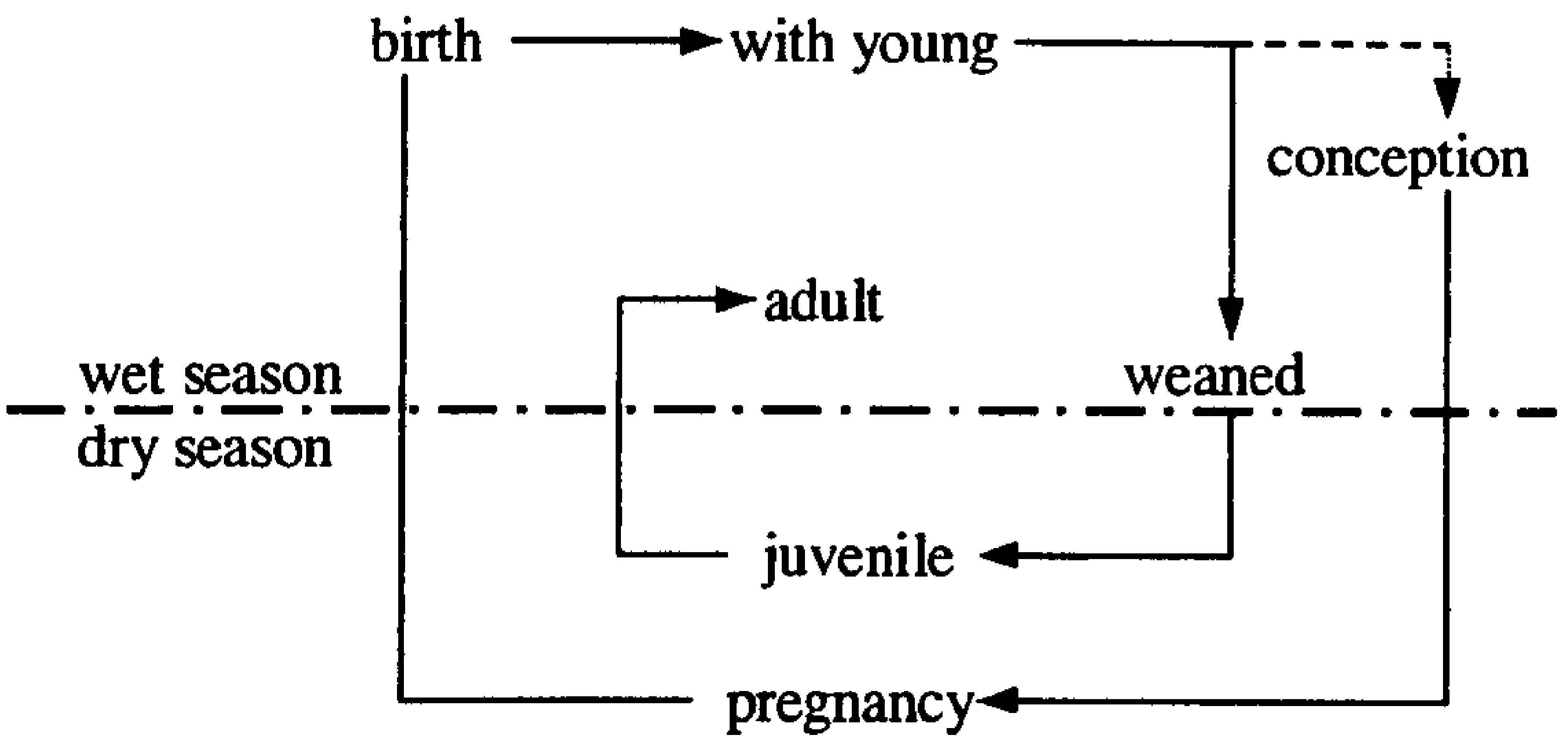

Figure 6.6 Recruitment cycle of impala. The dotted line indicates the parallel flow that allows females to carry out two processes simultaneously. Black lines indicate the process from conception to adult and the dot-dashed line separates the dry and wet season (Fraser 1968; Kayanja 1969; Spinage 1972; Jarmen & Jarmen 1974; Anderson 1975; Dunham & Murray 1982; Kindgon 1982b, 1997; Estes 1991; Stuart & Stuart 1997; Sinclair *et al.* 2000).

A further similarity between Grant's gazelle and impala, is that not only are impala recognised as mixed feeders, but they also have a similar feeding pattern (Talbot & Talbot 1962; Lamprey 1963; Hofmann 1973; Monro 1980; Kingdon 1982b, 1997; Hansen *et al.* 1985; Wronski 2002). For example, they tend to graze in the wet season and browse during the dry season (Azavedo & Agnew 1968; Dorst & Dandelot 1970; Sinclair 1977b; Delany & Happold 1979; Dunham 1980a; Estes 1991; Kingdon 1997; Stuart & Stuart 1997; Wronski 2002). Within the model the same set-up for Grant's gazelles was applied to impala. That is, they were treated like grazers without influencing the other grazing components.

6.2.6 Topi

Topi are exclusively grazers, and as such, compete with the migratory herbivore components during the dry season (Talbot & Talbot 1962; Dorst & Dandelot 1970; Stewart & Stewart 1970; Hansen *et al.* 1985; Estes 1991; Kingdon 1997; Stuart & Stuart 1997). It has been suggested that since topi only select new green grass, that the arrival of large numbers of migratory wildebeest greatly reduces the topis' food supply in a relatively short period of time (Kingdon 1982b). However, such selectively is not being considered at this stage of the model, although it is worth noting the wildebeest may be regulating topi populations more than it is possible to demonstrate in the model.

In terms of their reproductive cycle, topi appear to be similar to impala, with a birth peak at the start of the wet season and a intensive rut five months later (Gosling *et al.* 1987; Gosling & Petrie 1990). However, as a medium sized antelope (75 to 150 kg for females and 120 to 160 kg for males; Sachs 1967; Kingdom 1982b, 1997; Estes 1991; Stuart & Stuart 1997), it is unusual that juveniles become sexually mature by their first birthday despite not reaching their full size until a year and a half later (Figure 6.7; Fraser 1968; Child *et al.* 1972; Jewel 1972; Duncan 1975; Delany & Happold 1979; Western 1979). Consequently, since these females do not conceive until the rut, when they have reached 18 months age, only one juvenile survival curve was required for those individuals between 7 and 12 months of age (30.6 to 59.6 kg). The weight range for this curve was estimated using available birth weight data (10 to 13 kg; Georgiadis 1985; Kingdon 1982b).

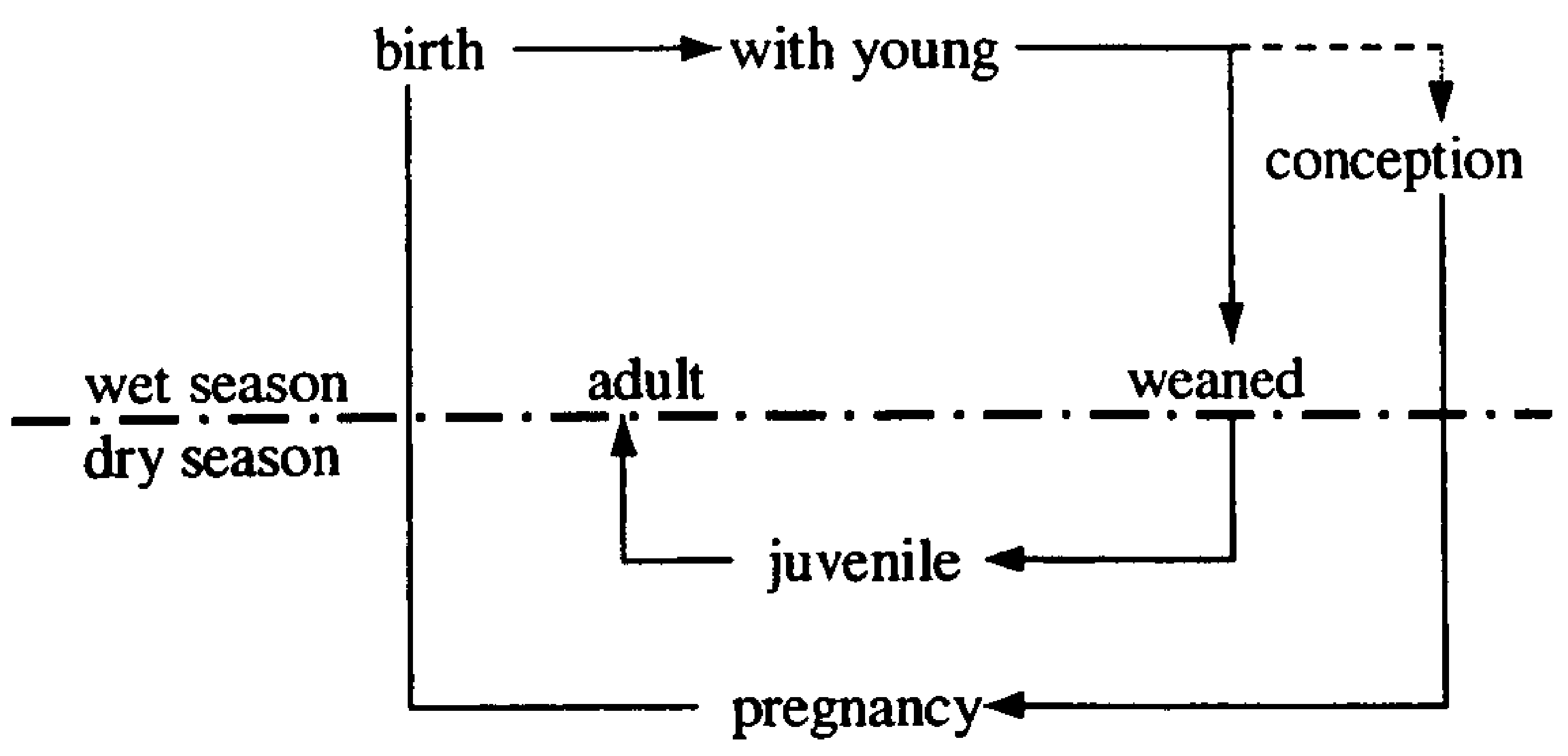

Figure 6.7 Recruitment cycle of topi. The dotted line indicates the parallel flow that allows females to carry out two processes simultaneously. Black lines indicate the process from conception to adult and the dot-dashed line separates the dry and wet season (Childs *et al.* 1972; Jewell 1972; Duncan 1975; Kingdon 1982b, 1997; Georgiadis 1985; Estes 1991; Stuart & Stuart 1997; Sinclair *et al.* 2000).

6.2.7 Hartebeest

Coke's hartebeest are exclusively grazers, found year-round in the same zones as topi, impala and buffalo and experience similar competitive pressures (Lamprey 1963; Dorst & Dandelot 1970; Stewart & Stewart 1970; Owaga 1975; Sinclair 1977b; Delany & Happold 1979; Kingdon 1982b, 1997; Hansen *et al.* 1985; Rodgers & Swai 1988; Estes 1991; Stuart & Stuart 1997). In terms of reproductive cycle hartebeest are very similar to their closest relative the topi, except that the time it takes for juveniles to reach sexual maturity is more representative of their size (116 to 185 kg for a females and 125 to 218 kg for males; Sachs 1967; Western 1979; Kingdom 1982b, 1997; Estes 1991). Additional juvenile recruitment survival curves were therefore required for 12 to 19 month-old juveniles (67.4 to 121.1 kg) and 19 to 24 month-old juveniles (87.5 to 161.2 kg). The weight ranges for these and 7 to 12 month-old juveniles (47.3 to 81 kg) were calculated using available information on hartebeest birth weight data (15.5 to 17.5 kg; Kingdon 1982b) and their adult weight range, attained at 24 months of age (Stanely-Price 1974; Delany & Happold 1979). Figure 6.8 illustrates their extended recruitment process.

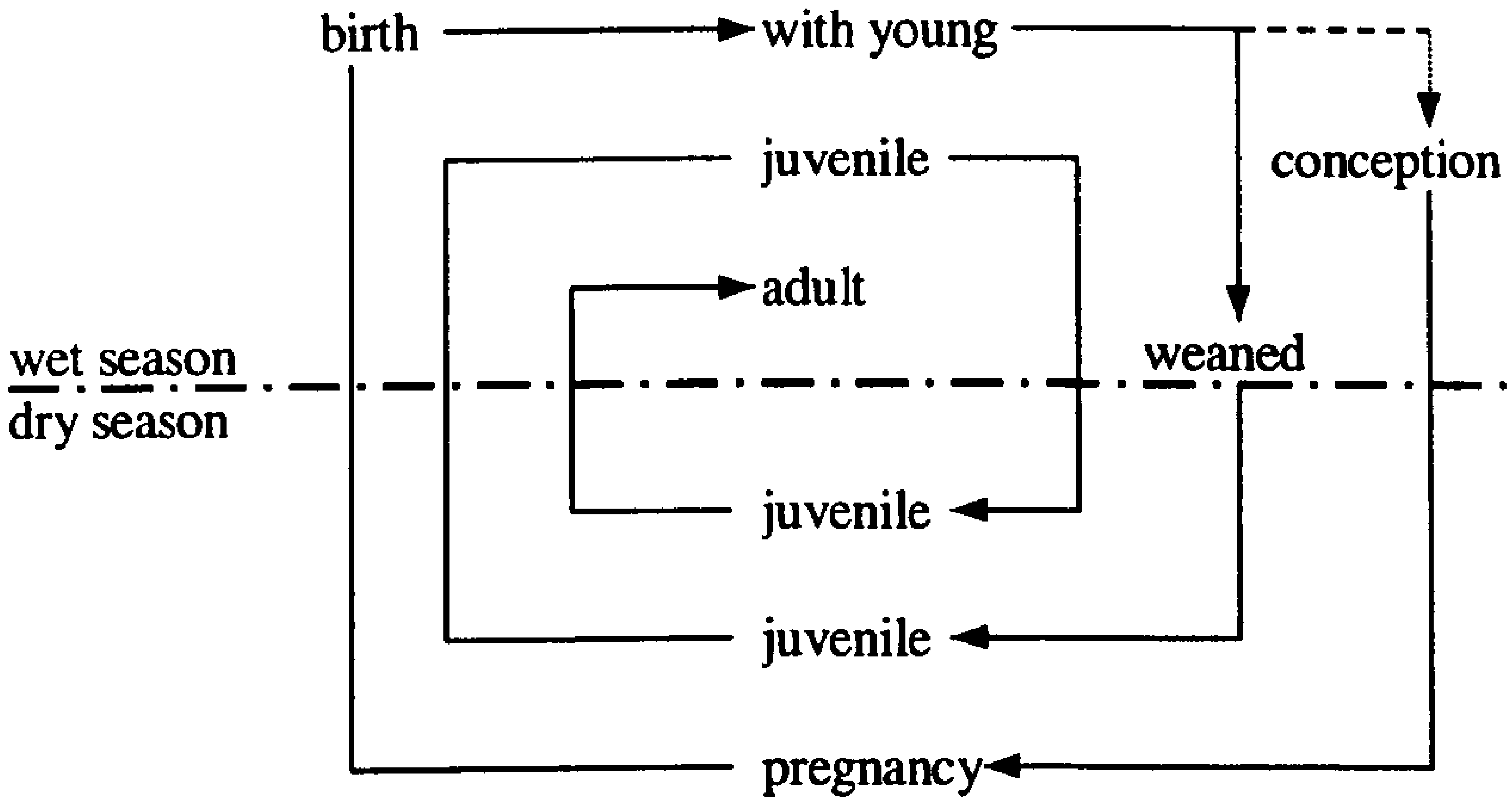

Figure 6.8 Recruitment cycle of hartebeest. The dotted line indicates the parallel flow that allows females to carry out two processes simultaneously. Black lines indicate the process from conception to adult and the dot-dashed line separates the dry and wet season (Leuthold & Leuthold 1975; Kingdon 1982b, 1997; Estes 1991; Stuart & Stuart 1997).

6.2.8 Resident wildebeest, zebra and Thomson's gazelle

The resident counterparts of the three migratory herbivore components were also added into the model. All three reside solely in zones 1 and 2, competing with their migratory compeers during the dry seasons and other resident components all year round (Fryxell *et al.* 1988). Within the model, reproductive strategies, and therefore survival curves, are the same as their equivalent migratory components.

6.2.9 Population numbers & sex ratios

Once all the above herbivore components were set-up, the model was initiated using population numbers for each in the dry season of 1960. These were taken from 1960 census data or from the nearest available year. However, in many instances census data for juveniles and young was not available. Where this was the case, available data on the reproductive success and/or survival of these two groups were used to estimate population numbers. Furthermore, where a herbivore component inhabits more than one zone year round, but census data only provides a total population count, it was assumed that individuals were evenly distributed over the total inhabited area. Population numbers for each zone, therefore, varied depending on the size of that zone. Table 6.2 shows these resulting population numbers and their sources.

Table 6.2 Population numbers for each herbivore component in the dry season 1960.

Herbivore	Zone	Population numbers			References
		Adults	Juveniles	Young	
Buffalo	1	6,433	4,655	1,552	Grimsdell 1969; Sinclair 1973a; Hilborn *et al.* 1995
	2	8,067	5,844	1,948	
Migratory zebra	1 / 3	158,420	19,580	15,399	Klingel 1969; Spinage 1972; Smuts 1976; Sinclair & Norton-Griffiths 1982; Hilborn *et al* 1995; Saltz & Rubenstein 1995; Hack *et al.* 2002; Saltz 2002
Thomson's gazelle	2 / 3	500,000	87,150		Talbot & Stewart 1964; Schaller 1972; Bradley 1977; Sinclair & Norton-Griffiths 1982; Borner *et al.* 1987; Hilborn *et al.* 1995
Grant's gazelle	2	21,174	3,691	2,426	Watson 1965; Borner *et al.* 1987
	3	18,826	3,281	2,158	
Impala	1	17500	5168		Watson *et al.* 1969; Sinclair 1972; Dunham & Murray 1982; Boshe & Malima 1986; Rodgers & Swai 1988
	2	52500	15505		
Topi	1	11200	3920		Talbot & Stewart 1964; Watson 1965; Sinclair 1972; Duncan 1975; Rodgers & Swai 1988
	2	8800	3080		

Table 6.2 continued …..

Hartebeest	1	1800	630		Talbot & Stewart 1964; Watson 1965; Sinclair 1972; Gosling 1974
	2	1200	420		
Resident wildebeest	1	5783	870	1042	Stewart & Talbot 1962; Talbot & Stewart 1964; Serneels & Lambin 2001
	2	7255	1092	1306	
Resident zebra	1	83499	2435	8116	Talbot & Stewart 1964; Klingel 1969; Spinage 1972; Smuts 1976; Saltz & Rubenstein 1995; Hack *et al.* 2002; Saltz 2002
	2	104,745	3054	10,182	
Resident Thomson's gazelle	1	23,140	4,033		Talbot & Stewart 1964; Watson & Kerfoot 1964; Borner *et al.* 1987; McNaughton 1985; Onyeanusi 1989
	2	29,028	5060		

The final variable required to initially estimate the number of females and males in each component's adult population was their sex ratio. As with population numbers, these were taken from data collected as near to 1960 as possible. Table 6.3 shows the data used and their references. As resident wildebeest, zebra and Thomson's gazelle were assumed to have a very similar social organisation to their migratory counterparts, it was considered unnecessary to repeat their sex ratio information in table 6.3.

Table 6.3 Sex ratios for each of the herbivore components.

Herbivore	Proportion of females in adult population	References
Buffalo	0.5	Spinage 1972; Sinclair 1974a, 1977b; Prins 1989; Estes 1991
Zebra	0.5	Hack *et al.* 2002; Berger 1983; Saltz 2002 Spinage 1972
Thomson's gazelle	0.61	Brooks 1961; Estes 1967; Hvidberg-Hansen & de Vos 1971; Owen-Smith 1977; Walther 1978a, b; Kingdon 1982b; Gosling 1986; Fitzgibbon 1990; Parker 1990; Nowak 1995
Grant's gazelle	0.61	Brooks 1961; Estes 1967; Owen-Smith 1977; Walther 1978a, b; Kingdon 1982b; Gosling 1986; Parker 1990; Nowak 1995
Impala	0.55	Jarmen & Jarmen 1973; Boshe & Malima 1986
Topi	0.5	Jewell 1972
Hartebeest	0.5	Dowsett 1966; Gosling 1974; Stanely-Price 1974; Kingdon 1982b

6.3 Grazing competition

At this stage, competition for food has not yet been introduced to the model. In order to achieve this, the amount of available grass per animal (which is then used to estimate the seasonal survival of males, females and juveniles and recruitment rates) needs to be calculated from the total number of individuals at the start of a specific season in each zone. For example, the amount of food available to a male migratory wildebeest during the wet season in zone 1, will depend on the total number of adult and juvenile migratory wildebeest, migratory zebra, migratory Thomson's gazelle and Grant's gazelle (Table 6.4).

Table 6.4 Zone occupancy of grazing herbivore components in each season (Dorst & Dandelot 1970; Kingdon 1982b, 1997; McNaughton & Georgiadis 1986; Durant *et al.* 1988; Rodgers & Swai 1988; Estes 1991).

Zone	Dry season herbivore occupancy	Wet season herbivore occupancy
1	migratory wildebeest, migratory zebra, resident wildebeest, buffalo, impala, resident zebra, Coke's hartebeest, resident Thomson's gazelle, topi,	buffalo, resident wildebeest, impala, resident zebra, topi, Coke's hartebeest, resident Thomson's gazelle
2	buffalo, resident wildebeest, resident zebra, Coke's hartebeest, resident Thomson's gazelle, topi, migratory Thomson's gazelle	buffalo, resident wildebeest, impala, resident zebra, Coke's hartebeest, resident Thomson's gazelle, topi, Grant's gazelle
3	No grazing components present	Grant's gazelle, migratory wildebeest, migratory Thomson's gazelle, migratory zebra

Furthermore, as functional groups are being treated separately (section 5.2.2), because their intake rates and feeding capabilities vary, so must each component. For instance, as bite size is allometrically related to weight, larger animals will consume more grass per bite (Owen-Smith 1982; du Toit & Owen-Smith 1989). In order to account for this, *FpA* for each component must not only reflect the number of individuals exploiting the same resource but also the body size of each component. The average weight of each functional group and sex ratio within each component is used to calculate conversion values (see table 6.5), which in turn, can be used to convert seasonal population numbers of each component into equivalent population numbers for a specific component.

Table 6.5 Example of biomass conversion values used for male wildebeest (234 kg) based on the average weights of each component's functional groups.

	Average weight (kg)	Conversion values
Female wildebeest	200	0.85
Juvenile wildebeest	152	0.65
Male zebra	280	1.20
Female zebra	213	0.91

For example, when considering the survival of each functional group or sex in a particular component, such as male wildebeest, all other components are converted into male wildebeest equivalents. So 100 female wildebeest + 50 juvenile wildebeest + 20 male zebra + 20 female zebra become ([100 x 0.85] + [50 x 0.65] + [20 x 1.20] + [20 x 0.91]) 160 male wildebeest equivalents. The total number of male wildebeest and male equivalents can then be used to calculate the amount of green grass available to male wildebeest throughout that season.

For the purposes of this model, zebra were considered to be non-selective feeders. The amount of green grass they consume depends on the proportion of green grass to dry grass available at the time. Consequently, the amount of green grass consumed by zebra varies depending on this proportion, which in turn, influences the degree of competition that occurs between zebra and the other components. This is incorporated into the model by assuming that the number of zebra feeding on green grass is equal to the proportion of green grass in the zebra's diet each season. For instance, if green grass constitutes 30 % of the total amount grass, then 30 % of the zebra population have a diet of green grass. This figure represents the number of zebra to be converted into the appropriate component's equivalents. Similarly, as the other components, excluding Grant's gazelle and impala during the dry season, are taking only the green grass proportion of zebra's diet, their population numbers, when converted to zebra equivalents, also represent this proportion.

The amount of grass available will also depend on the amount of grass grazed (see section 5.5). Like wildebeest, the maximum amount of grass that can be grazed by each component was estimated using population numbers at the start of each season and the maximum rate of energy expenditure possible during recruitment (McNab 1980, Clutton-Brock *et al.* 1989). For most of the components, conception whilst with young proved to be the most energetically expensive recruitment process. Only zebra and buffalo were similar to wildebeest, in that pregnancy was the most costly process when they had 4 to 6 month old young and 7 to 12 month old young respectively.

Once this link between the amount of grass available and the number of grazing herbivores present has been established, the model can be run. However, it will only predict seasonal population numbers for each of the components when competition for a common food resource is the only regulating factor. The next stage of the model is to include another principal regulating factor, predation (Sinclair 1985; Fryxell *et al.* 1988). The influence this has on herbivore population numbers is established in the following chapter, and the results of these two chapters will be discussed further in chapter 8.

CHAPTER 7:PREDATION EFFECTS

7.1 INTRODUCTION

The impact of mammalian predators on their prey is a complex and, at times, controversial aspect of ecology (Talbot & Talbot 1963; Kruuk 1969; Sinclair 1970; Smuts 1978; Mills & Shenk 1992). The Serengeti-Mara ecosystem is an excellent example of this complexity and its general pattern of predator-prey relations has only recently been elucidated. For instance, if the Serengeti were a simple predator regulated system, one would expect to find each predator population limited by their food resources (Slobodkin *et al.* 1967; East 1984). Consequently, the biomass of the carnivore species present would be closely correlated with the biomass of their prey and corresponding cyclical fluctuations would occur between both predator and prey populations (Varley & Gradwell 1963). However, a study initiated in July 1964 on the feeding habits of spotted hyaenas as part of the Serengeti Research Project, evinced that in 1965 and 1966, spotted hyaenas caused only a small part (less than 17 %) of the total mortality of adult wildebeest (Kruuk 1966b; 1969). This led to the belief that population regulation through predation was of little importance in the Serengeti as the presence of large populations of wildebeest, zebra and Thomson's gazelle, as the main food supply, saturated the degree of predation (Kruuk 1969; Sinclair 1970; Braun 1973; Houston 1979; McNaughton & Georgiadis 1986; Kelly *et al.* 1998). The fact that predators did not occur in large enough numbers to assert any considerable mortality pressure on these migrant populations implies that they themselves are either not being regulated by food or at least not by these particular prey populations (Kruuk & Turner 1967).

Kruuk (1972) suggests that the migratory habits of wildebeest, zebra and Thomson's gazelle causes a sudden reduction in the abundance of food available to predators. Since Serengeti carnivores do not follow these annual migrations, they are dependent on resident prey species during the absence of the migrant ungulates (Bertram 1973; Hanby & Bygott 1979; Viljoen 1993; Hanby *et al.* 1995; Mills *et al.* 1995). Unlike migrants, resident herbivores have low population densities and as such prevent predators from reaching a population level where they might exert a controlling influence on migratory prey populations (Kruuk 1969, 1972; Schaller 1972; Sinclair 1972; Braun 1973; Sinclair *et al.* 1985; van Orsdol *et al.* 1985; Mills & Shenk 1992; Hanby *et al.* 1995). Consequently, resident herbivore populations are more heavily influenced by predation when the migrants are not present, which in turn affects their population turn-over (Bertram 1973; Sinclair 1985; Fryxell *et al.* 1988; Mills & Shenk 1992).

Having said this, further research has revealed that it maybe a fallacy to assume that if predators can not regulate migrant wildebeest numbers, then by implication, the same reasoning applies to migrant zebra and Thomson's gazelle (Kruuk 1972; Sinclair 1979b). Initial studies carried out by Schaller (1972) showed that predation of zebra by hyaenas accounted for 59 % to 74 % of annual mortality. Further studies by Sinclair & Norton-Griffiths (1982) determined that such a predation rate had two to three times more impact on zebra numbers than on wildebeest numbers, and suggested that this magnitude of predation is enough to regulate the zebra population. It was even postulated that such predation pressure has prevented the zebra population from increasing (Sinclair & Norton-Griffiths 1982; Senzota 1988). In a similar study, Borner *et al.* (1987) found that since the early 1970s an increase in predator numbers, and a concomitant decrease in migrant Thomson's gazelle, has led to a growing predation impact on the Thomson's gazelle population. They also concluded that the increasing annual take-off of Thomson's gazelle by predators became a regulating factor. It is therefore not necessarily the migratory strategy used by wildebeest that precludes them from being regulated by their predators, but rather their very high population density in relation to their predator population density.

Even though regulation through predation is not a principal mortality factor of migrant wildebeest, its influence on all the competing herbivore populations is still important to the ecosystem dynamics and may have an indirect affect on wildebeest numbers (Smuts 1978). By including predation into the model at this stage, further elucidation of the natural ecosystem's functioning may be achieved (Sinclair 1972). This chapter deals with the incorporation of predation into the model and the impact it has on herbivore population dynamics is then discussed in chapter 8.

7.2 PREDATION RATE

In order to estimate the seasonal take-off of herbivores by the five main large carnivore components within the Serengeti ecosystem (lions, spotted hyaenas, leopards, cheetahs and African wild dogs) certain parameters are required. These include the amount of prey required by an individual carnivore species in a specific season, the percentage of prey in each carnivore's diet with respect to species, sex, age, condition, season and location within the Serengeti, and finally, the number of predators present each season (Mills & Shenk 1992).

7.2.1 Metabolic rates of each carnivore species

In this part of the model metabolic rates can be used again (see section 5.3.1) as indicators of the amount of food required by each carnivore component. That is, the total amount of energy a particular carnivore requires just to stay alive is satisfied when that carnivore consumes a certain amount of prey (Peter 1983; Campbell 1996). This minimum amount of prey required by each carnivore species can be assumed to approximate the amount of prey consumed.

As with herbivores, the metabolic rate of each carnivore component can be calculated using a log linear equation describing the relationship between basal metabolic rate (BMR) and body mass (equation 5.4; Hayssen & Lacy 1985; Gichohi *et al.* 1996). Hayssen & Lacy (1985) give the coefficients specifically describing this relationship for the order Carnivora (Appendix table 2). The average BMR of each carnivore species in the model can be calculated using equation 5.4, the coefficients for the intercept (a) and slope (b) for the Order Carnivora (0.630 & -0.262 respectively; Appendix table 2) and the average weight of each carnivore given in table 7.1.

Table 7.1 Range and average body weights of the five large mammal carnivores (Maberly 1966; McLaughlin 1970; Bertram 1975, 1982; Estes 1976, 1991; Kingdon 1977, 1997; Caro & Collins 1987; Creel & Creel 1996; Stuart & Stuart 1997)

	Weight in kg		
	Minimum	Maximum	Average
Lion	110	290	200
Spotted hyaena	40	90	65
Leopard	17	90	53.5
Cheetah	30	72	51
African wild dog	17	36	26.5

The BMR value can then be converted into a daily megajoule equivalent using equation 5.5 and finally converted into realised metabolic rate (RMR) by multiplying this equivalent figure by 3 (see section 5.3.1). Since Hayssen & Lacy's (1985) study, the metabolic rates of various Carnivora species have been measured and this data can be used to test the accuracy of the estimated RMRs (Figure 7.1).

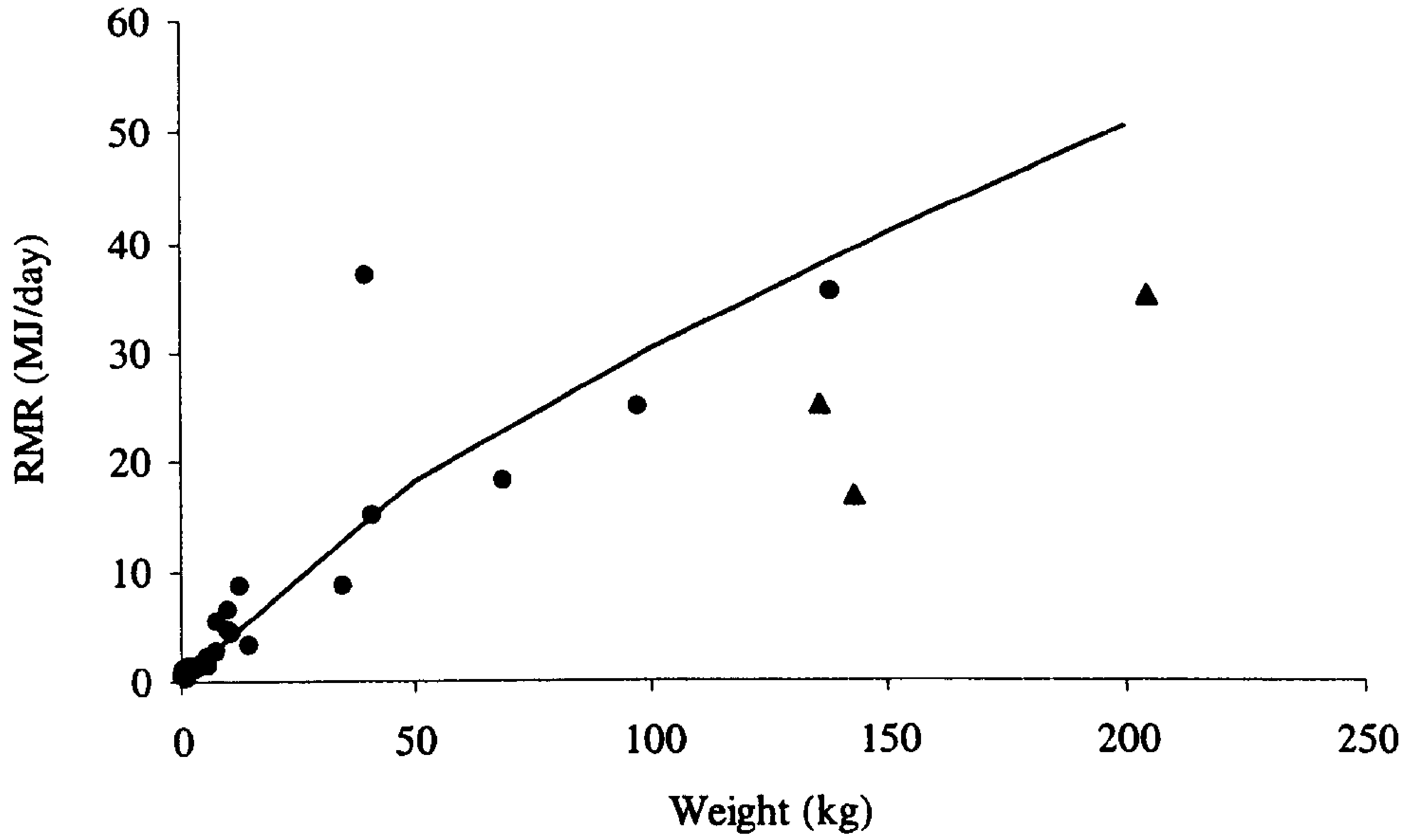

Figure 7.1 Comparison between RMRs for various carnivores given by McNab 1996 (points) and RMRs estimated using Hayssen & Lacy's (1985) equation (line). The triangles represent Ursidae species.

An analysis of covariance, revealed a significant difference between the sourced RMR data and that calculated using Hayssen & Lacy's (1985) equation (F value = 4.354, $P < 0.05$). Interestingly, the points that do not appear to fit the estimated line in figure 7.1, are from the Ursidae family (shown as triangles). If these three points are omitted and the ANCOVA repeated, there is no significant difference between the sourced data and the estimated line (F = 0.06, $P > 0.05$). One explanation for this change in significance is that carnivore metabolic rates are not solely influenced by size, but also by food habits, activity levels and climate (McNab 1980, 1996). It is possible that these factors are contributing to the dissonance in the metabolic rates of the Ursidae species.

Furthermore, as Ursidae species are not present in the Serengeti or in fact Africa, their RMR values are not actually relevant to the model. Hayssen and Lacy's (1985) coefficients can therefore be used with confidence to calculate the daily RMR for each of the carnivore components (Table 7.2).

Table 7.2 Estimated daily RMR for each carnivore component based on their average weights.

	RMR (MJ/day)
Lion	50.4
Spotted hyaena	22.0
Leopard	19.1
Cheetah	18.4
African wild dog	11.4

Of course, in order to calculate the average amount of meat each carnivore needs to satisfy its metabolic demands, the metabolic content of its food source is required. Conveniently, Ledger (1968) gives the calorific value of boneless herbivore meat in the Serengeti, all except for zebra (Table 7.3). As the calorific value of zebra meat is not currently available, an average figure was used as a representative. Furthermore, for the purposes of this model it was assumed that these values corresponded to the metabolisable energy content (ME) of the meat.

Table 7.3 Metabolic energy content of different herbivore component meat in the Serengeti, as measured by Ledger (1968). * the figure for zebra represents an average ,as no data was available.

	Metabolic energy content of meat (wet weight MJ/kg)
Wildebeest	4.65
Zebra	4.64*
Thomson's gazelle	4.27
Grant's gazelle	4.65
Impala	4.27
Topi	4.44
Coke's hartebeest	4.35
Buffalo	5.86

One consequence of the varying ME contents of prey species's meat is that the amount of food a particular carnivore is required to eat to meet its metabolic demands depends on the species of herbivore it feeds upon. Therefore, the next step is to find out the general seasonal diet composition of each carnivore component.

7.2.2. Prey preference

Studies on predator-prey relationships have shown that two factors govern the diet composition of carnivores; active selection of more profitable prey and encounter rate (Scheel 1994). Of course, physiology and behaviour determine the general characteristics of prey included in a carnivore's diet (Schaller 1972). In other words, a carnivore's prey selection is influenced by adaptations derived through their evolutionary history. Each predator species has been shaped and refined by natural selection to maximise nutrient intake within the bounds of a wide range of ecological constraints (East 1984; Sunquist & Sunquist 1996). For example, characteristics of prey species, such as their abundance, temporal and spatial distribution, size, defences and anti-predator tactics, represent a number of constraints (East 1984; Sunquist & Sunquist 1996; Sinclair *et al.*2000). Other constraints include the distribution and abundance of hunting cover, climatic conditions, and the presence and abundance of congeners and other potential competitors (Kruuk 1972; Schaller 1972; Bertram 1973; East 1984). Consequently, the basic task of finding and gathering food under these constraints fundamentally affects a species' spacing patterns, the structure of its social systems and its hunting strategy (Schaller 1972; Bertram 1973; Sunquist & Sunquist 1996).

7.2.2.1 Lions

Unlike most Felidae, lions form fairly cohesive social units, called prides (Kingdon 1977, 1997; Ogutu & Dublin 2002). Each pride consists of one to four adult males, several adult females and a number of sub-adults and cubs. It constitutes a relatively stable unit, the composition of which is mainly affected by deaths, the acceptance of young females that have grown up in the pride, the expulsion of young males from it and the intermittent change in pride tenure by adult males (Schaller 1972; Bertram 1976). Males are the most transitory members of prides, and often form nomadic coalitions when not holding one (Bertram 1973, 1976). The evolution of such a social system is still under debate even though it has been studied extensively (Kruuk & Turner 1967; Schaller 1972; Packer & Ruttan 1988; Gittleman 1996). What these studies have revealed is that the occurrence of this social behaviour has enabled lions to exploit certain prey species that the other carnivore components cannot (Schaller 1972; Kruuk 1975; Kingdon 1977). By hunting with pride members, lions may have greater success at locating and catching prey. For example, Schaller (1972) found that African lions had a higher success rate in capturing Thomson's gazelle, zebra and wildebeest when two or more lionesses hunted together. It has also allowed them to be catholic in their choice of prey, both in diversity and size (Schaller 1972; Kruuk 1975, Kingdon 1977; Packer & Ruttan 1988; Gittleman 1996). For instance, as the biggest carnivore in the Serengeti, the combined weight of a hunting group enables lions to include larger prey species in their diet (prey weighting > 200 kg; Kruuk & Turner 1967; Caraco & Wolf 1975; Prins & Iason 1989). Both Schaller (1972) and Bertram (1979) observed that hunting groups frequently attacked adult buffaloes, whereas a single lion rarely attempted it.

However, there appears to be a continued dispute as to whether communal hunting is an organised event or a coincidence, and that any help lions give each other is inadvertent (Kruuk & Turner 1967, Schaller 1972; Kingdon 1977). In truth, the actual complexity of communal hunts lies between the two extremes (Schaller 1972). What is clear is that the hunting strategy employed by lions enables them to hunt successfully both individually and in groups (Kruuk & Turner 1967). A hunt generally starts with a search, not directed at any particular animal or group of animals, in which lions scan the environment either from a sitting position or in a slow walk. Once a potential quarry is identified, lions can ambush it, by hiding and waiting for the prey to move closer, or stalk up on it. When prey is within 10 m to 60 m lions will rush in and drag the prey down by their own weight, eventually killing it, usually through suffocation (Kruuk & Turner 1967; Kingdon 1977). Observational evidence suggests that there is some degree of co-ordination between a group of hunting lions (Schaller 1972). When several individuals spot potential quarry they characteristically fan out and approach in a broad front. Schaller (1972) states although this is perceived as co-operation, lions are simply orienting towards a common goal. However, by exhibiting the same behaviour in a relatively organised fashion it increases the hunting success rate of those lions involved. If hunting lions were acting independently of each other, then larger species would not be considered as potential prey (Bertram 1979). It appears that the presence of other lions may lead to the successful capture of prey that would otherwise be physically impossible.

7.2.2.2 Leopards

As solitary hunters, leopards are limited to the prey species that they are physically capable of bringing down on their own (Schaller 1972; Bertram 1982; Macdonald 1983; Sandell 1996). Despite this, the composition of their diets varies more than that of lions, as they will regularly feed on anything from dung beetles to medium-sized antelopes (< 200 kg; Fey 1964; Schaller 1972; Bertram 1982; Nowell & Jackson 1996). Although as opportunists, leopards have been reported to take vulnerable prey weighting up to 900 kg (Kingdon 1977; Bertram 1982; Nowell & Jackson 1996). One principal advantage of their generalist diet is that they have the ability to adapt to changes in prey availability with ease (Nowell & Jackson 1996).

Like lions, leopards hunt by stalking or ambushing, relying on concealment until their prey is close enough to catch successfully (Schaller 1972; Kingdon 1977). The leopard is essentially a woodland inhabitant, and in order to hunt effectively in this type of environment, it requires stealth and camouflaging (Kruuk & Turner 1967; le Roux & Skinner 1989; Nowell & Jackson 1996). Hence, its coat appears to mimic the dapple of leaves and their shadows (Kingdon 1977; also refer back to section 1.5.7). While this coloration is an advantage in the presence of trees, broken terrain, thickets and other heavy vegetation, leopards are rather conspicuous when out in the open (Nowell & Jackson 1996). As a consequence, they are relatively restricted to these closed environments. However, as the only large carnivore specially adapted to live and hunt in such habitat types, it occupies this niche on its own, enduring relatively little competition from any other large carnivore (Kruuk & Turner 1967; Schaller 1972; Kingdon 1977; Bertram 1982; Nowell & Jackson 1996).

7.2.2.3 Cheetahs

In some aspects, cheetahs are very similar to leopards, they are approximately the same weight and both live a comparatively solitary existence, although adolescent and adult male coalitions are not uncommon (Kingdon 1977; Caro & Collins 1986; Caro 1994; Nowell & Jackson 1996). However, in other aspects, they are very different. For example, in comparison to leopards, cheetahs have deep chests with enlarged bronchi, lungs, and heart, allowing them to run for longer distances and at a high pace (Eaton 1974; Gonyea 1976; Caro 1994; Nowell & Jackson 1996). In addition, they are more streamlined, have proportionally longer limbs, a flexible spine to increase stride length, a long tail for balance and an enlarged nasal aperture for increased air intake (Hildebrand 1959, 1961; Caro 1994; Nowell & Jackson 1996). Even their paws possess adaptations for sudden braking, traction and skid prevention, such as hardened and pointed digital and metacarpal pads, permanently exposed claws and longitudinal ridges in their palmar pads.

However, the cheetah's light build restricts the size of prey it can handle (< 80 kg; (Schaller 1968; Macdonald 1983; Packer & Ruttan 1988; Caro 1994; Gittleman 1996; Sandell 1996). Unlike leopards and lions, it does not possess the upper body strength required to drag down large prey. Instead, a cheetah relies on agility and quick reflexes. A hunt is initiated in a similar way to that of a lion's, by scanning the environment, although cheetahs tend to conduct this activity from a clear vantage point. It is believed that during this surveillance a cheetah may already be selecting an individual prey animal to target (Kingdon 1977). Following this, a cheetah begins to stalk the quarry, then breaks into a sprint depending on its assessment of the circumstances (Kruuk & Turner 1967; Schaller 1968; Kingdon 1977; Caro 1994). This naturally causes prey to panic, scatter or stampede, but this is an advantage to the cheetah. By forcing a prey animal to flee it reduces its balance, enabling a cheetah, if it is close enough, to hook one of its prey's legs from under it (Kruuk & Turner 1967; Kingdon 1977). In the few seconds in which an animal is lying on its back or side a cheetah can quickly attain a strangle hold and suffocate it (Kingdon 1977; Caro 1994; Nowell & Jackson 1996). Of course, this hunting technique is impeded, if not impossible, when the surrounding vegetation is too dense. Consequently, cheetahs thrive on open plains or lightly wooded and open woodland areas (Kruuk & Turner 1967; Kingdon 1977; Nowell & Jackson 1996).

7.2.2.4 Wild Dogs

African wild dogs employ a similar hunting strategy to that of the cheetah and subsequently endure similar habitat restrictions (Kingdon 1977; Fanshawe & FitzGibbon 1993; Creel & Creel 1995). However, although they may frequent the same habitat types, there is little competition between these two predators (Mills & Biggs 1993). For instance, even though African wild dogs are the smallest large predator in the Serengeti, they are capable of handling medium-sized prey (up to 200 kg in weight; Creel & Creel 1995; Malcolm & van Lawick 1975; Woodroffe *et al.* 1997). This is because, like lions, they partake in communal hunting as part of their intense social behaviour. They form non-territorial cohesive social units based on equality rather than a firm hierarchy, although only an alpha pair generally reproduce (Kuhme 1965; Estes & Goddard 1967; Schaller 1972; Sheldon 1992; Woodroffe *et al.* 1997). Consequently, all individuals equally share duties, from care of pups to hunting (Schaller 1972; Malcolm 1979; Malcolm & Marten 1982; Woodroffe *et al.* 1997). The latter appears to be an extremely well-organised activity and one of the most striking aspects of dog society. A hunt is initiated by what is referred to as a 'social rally' (Kingdon 1977). During this there are high levels of physical contact and vocalisation, thought to coordinate the pack in preparation for hunting (Estes & Goddard 1967; Kuhme 1965; Kingdon 1977; Woodroffe *et al.* 1997). The wild dogs then proceed to set out on a hunt, initially moving in single file, although it is not long before they begin to spread loosely over the terrain. While this swiping strategy is good for flushing out potential prey laying hidden, it also increases the chance of spotting a herd of potential prey (Schaller 1972). Once a herd is located, the dogs trot towards it in a broad front, and like cheetahs, suddenly break into a chase (Kingdon 1977). As the prey panic and scatter, those that lag or are isolated become quarry candidates and a separate dog concentrates on chasing each. By pursuing these different individuals the dogs appear to be conducting a selection process, in which the reactions and stamina of each quarry are tested (Schaller 1972; Kingdon 1977). The quarry considered to be the most suitable target then becomes the focus of all the dogs pursuit. During this chase, one or two dogs pursue the quarry at anyone time, while the other dogs position themselves around the running prey, ready to intercept were it to suddenly change direction or to relieve a pursuing dog (Estes & Goddard 1967). An individual dog can sustain a high speed chase for much longer than a cheetah and this length of time is further extended when each dog takes a turn (Taylor *et al.* 1971; Kingdon 1977; Woodroffe *et al.* 1997). By sustaining the pursuit of their prey, at some point the quarry becomes too exhausted to continue running. As it slows the dogs bring it to a halt and immediately start to feed on the helpless, exhausted prey (Kuhme 1965; Kingdon 1977; Creel & Creel 1995;Woodroffe *et al.*1997). One interesting aspect of their social behaviour is that each dog receives a relatively equal portion of every kill, even those not involved in the hunt (Schaller 1972).

7.2.2.5 Spotted hyaena

In contrast to wild dogs, the amount of food individual spotted hyaenas receive at a kill, depends on their position in their female dominated hierarchy. Like lions and African wild dogs, hyaenas live in social groups called clans (Kruuk 1972; Schaller 1972; Tilson & Hamilton 1984; Frank 1986; Hofer & East 1993a, 1995; Hofer 1998). The common goal of clan members is to defend their territory and dens (Kingdon 1977; Hofer 1998). During the intervals when individuals are not on guard duty they can go in search of food, which can be a very independent activity or a very social activity (Kruuk 1972; Schaller 1972; Hofer 1998). The level of coordination between hyaenas seems similar to that of lions and this becomes very apparent when a kill has been made. Initially, each individual tries to eat more and faster than its hunting companions (Kruuk 1972; Kingdon 1977). However, before long, those individuals that are higher in the hierarchy system begin to displace less dominant individuals from the kill (Kruuk 1972; Kingdon 1977). Furthermore, dominant individuals can arrive after a kill is made and still usurp inferior clan members (Kruuk 1972; Kingdon 1977).

In Africa, spotted hyaenas are considered to be the most numerous large carnivore (Kruuk 1972; Kingdon 1977; Hofer 1998). One reason for this is that they are adaptable and opportunistic hunters, so any sized animal can be potential prey (Kruuk 1972; Lamprecht 1981). Not only do they have the ability to recognise vulnerability and quickly target those individuals that are weak, diseased or injured, but they are also quick to recognise and react to a healthy individual in a vulnerable position (Kruuk 1972; Estes 1976; Kingdon 1977; FitzGibbon 1989b; Hofer 1998). By varying their hunting tactics to suit the situation, hyaena can successfully take advantage of any opportunity. For example, when an animal is isolated or resting, hyaenas have been observed to stalk or ambush prey like lions and leopards (Kruuk 1972; Schaller 1972; Hofer 1998). On the other hand, when a hyaena targets a vulnerable individual within a herd, it can chase that animal down even over a long distance, like a wild dog (Kruuk 1972; Schaller 1972; Hofer 1998). Their success at either of these two hunting methods is increased by the number of hyaenas present (Hofer 1998).

7.2.2.6 Prey selection

Although it is these various behavioural and physical adaptations within each carnivore component that dictate the general characteristics of prey in their diet. The selection of prey of specific ages, sex and species is principally determined by encounter rate and opportunity (Scheel 1994). The former is simply a case of prey abundance, the more likely it is to encounter a particular type of prey, the more likely it will constitute a greater proportion of a carnivore's diet (Walther 1969). This is certainty reflected in the diet composition of each carnivore component in the Serengeti. For instance, either wildebeest, zebra or Thomson's gazelle, the three most abundant herbivore species in the ecosystem, are annually the most commonly eaten prey of all five large carnivores (Kruuk & Turner 1967; Schaller 1968; Bertram 1982; East 1984). However, the migratory behaviour of these three herbivores has important consequences on seasonal diet composition (Maddock 1979; Bertram 1982; Hofer & East 1993a, 1995; Hanby *et al.* 1995). Once migrants have left an area, it is the most abundant resident components that are more frequently predated (Figure 7.2; Kruuk & Turner 1967; Schaller 1972; Hanby & Bygott 1979; Bertram 1982; Hofer & East 1993a; Sunquist & Sunquist 1996; Cooper *et al.* 1999).

Furthermore, the occurrence of seasonal reproduction amongst herbivore components causes a considerable fluctuation in diet composition of carnivores (Kruuk & Turner 1967). For example, synchronising births to reduce the proportion of new-born young lost is an anti-predator adaptation saturating carnivores with potential prey. Subsequently, during these periods young become the most abundant and therefore, the most consumed food source (Talbot & Talbot 1963; Watson 1966; Sinclair *et al.* 2000).

Optimal diet theory not only predicts that the inclusion of a prey type in the diet depends on the encounter rate, but also profitability (FitzGibbon 1990; Scheel 1994). In other words, those prey that provide the largest energetic intake at a minimal expenditure (FitzGibbon 1990). If this is the case, carnivores should actively select those animals that are more vulnerable, and evidence from a number of studies suggests that this does occur to varying degrees. As opportunists, it is in the nature of spotted hyaenas to target weaker individuals within a herd or those in a vulnerable position (Estes 1976; Kingdon 1977; FitzGibbon 1989b). In comparison, Scheel (1994) revealed that lions take a higher proportion of some prey species than expected based on random samples of the prey population, and concluded that they were activity seeking certain prey.

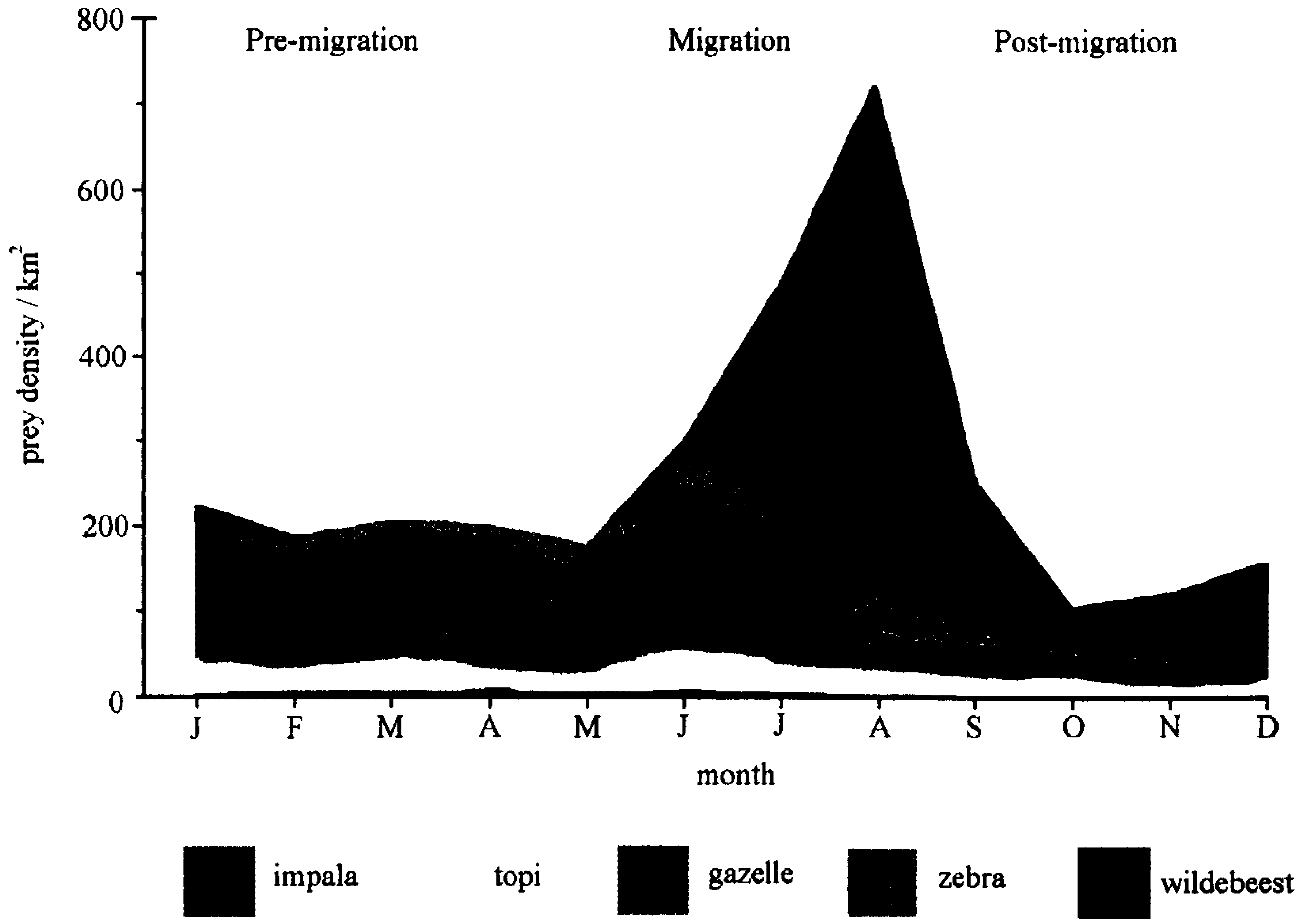

Figure 7.2 Temporal variation in the abundance of common ungulate species in the northern region of zone 1 (Cooper *et al.* 1999).

The selection by predators of one prey animal over another appears to be based on two factors, behaviour and physical state, and both can vary considerably between species, sex and age groups (Kruuk 1972; Schaller 1972; FitzGibbon 1989b, 1990). In the Serengeti, the composition of each carnivore's diet is certainly a good indicator of which types of prey are most vulnerable and when. For example, Walther (1969) claimed that Thomson's gazelle are relatively easy to hunt in comparison to all the other antelopes and this he reasoned was why they were the principal constituent of all the major carnivores' diets. FitzGibbon (1990) goes on to state that of those Thomson's gazelles taken by predators, the number of males killed exceeded that expected from the sex ratio of the local population. FitzGibbon (1989b; 1990) suggests that this is because predators target individuals that are either positioned on the periphery of groups, further from their nearest neighbours, in areas of high vegetation, less vigilant or are in small groups or on their own, and these are generally male. The fact that males are found in more vulnerable situations is a consequence of their social behaviour (Rudnai 1974; FitzGibbon 1990). Like many ungulate species, Thomson's gazelle's social system is a form of resource-defence polygyny (Rudnai 1974; Gosling 1986). Here, females and their offspring form large, relatively stable groups, while males normally form small bachelor groups until the breeding season when they compete for these females or the areas that females visit (Brooks 1961, Estes 1967; Estes & Goddard 1967; Hvidberg-Hansen & de Vos 1971; Walther 1978b; FitzGibbon 1990). Furthermore, once young males are weaned they are forced to leave the female herds. In the days following this, they are not only physically vulnerable, suffering from exhaustion and possibly injury incurred during their eviction, but they also remain on the outskirts of their maternal herd (Dowsett 1966; Jarman & Jarman 1973; Gosling 1974, Stanely-Price 1974; Kingdon 1982b). They therefore become more vulnerable to predators than their female counterparts within the herd (Rudnai 1974). It is, therefore, not surprising that sex-bias predation similar to that of Thomson's gazelle's has been reported in impala, wildebeest and hartebeest (Kruuk & Turner 1967; Jarman & Jarman 1973; Rudnai 1974; Kingdon 1982b).

Age appears to be the most defining aspect of prey selection by the Serengeti's large carnivores. Once it has been separated from its mother, a new-born of any species is easy prey for predators, as it has very little stamina, puts up little resistance and its size makes it easier to handle by predators (Jarman 1976). Consequently, new-born young feature quite significantly in the diets of each carnivore component, although their availability can be limited by birth synchronicity (Talbot & Talbot 1963; Kruuk 1969; Estes 1976; Hofer *et al.* 1993). As young get older, their stamina, resistance and experience increases, and they become less profitable to catch as 'handling time' increases. For example, Estes (1966) found that older wildebeest calves were virtually ignored by hyaena, who consistently went for new-born calves. However, when the birthing period is over, the older young and even juveniles, became the targets of predators as they are still less successful at escaping in comparison to adults in their prime (Schaller 1972; Rudnai 1974; Hofer *et al.* 1993).

The seasonal diet composition of the Serengeti's five large carnivores is, therefore, governed by the variation in availability of profitable prey. Consequently, a carnivore's diet reflects the presence of resident species, the presence and absence of migrants, occurrence and coordination of reproductive events and the difference in behaviour of individuals within a species (Viljoen 1993; Hofer & East 1995). Not only may all these factors vary depending on the season, but also on the zone. As a result, the diet composition of carnivores within each module is subject to variation (Elton & Greenwood 1987). Figures 7.3 to 7.7 were created to illustrate the estimated seasonal composition of each carnivore component's diet in each zone as a percentage, based on available information found in the literature (Wright 1960; Estes & Goddard 1967; Kruuk & Turner 1967; Kruuk 1969, 1972; Jarman 1972; Schaller 1972; Malcolm & Van Lawick 1975; Kingdon 1977; Bertram 1982; Bourlière 1983; Caro & Collins 1986; East 1984; Frame 1986; Ammann 1987; FitzGibbon 1989b; 1990, 1994; Dunham 1992; Sheldon 1992; Hofer *et al.* 1993; Woodroffe *et al.* 1997; Caro 1994; Hofer 1998; Cooper *et al.* 1999). In defining these estimated values, two assumptions were made. The first was that as each carnivore's diet is primarily composed of herbivore species that are included in the model, those species not included in the model were disregarded at this stage (Kruuk 1972; Schaller 1972; Caro 1994; Nowell & Jackson 1996; Woodroffe *et al.* 1997). The second assumption was that, like the resident herbivore components, carnivores could not move between zones (see section 6.1). One exception to this is that during the dry season, resident carnivores in zone 3 not only preyed on its resident herbivores, but also those in zone 2. Investigations have shown that in the dry season most carnivores on the plains (zone 3) do in fact extend their ranges or abandon their territories completely in the absence of the migrant herbivores (Kruuk 1972; Schaller 1972; Bertram 1973; Kingdon 1977; Hanby & Bygott 1979; van Orsdol *et al.* 1985; Durant *et al.* 1988; Hofer & East 1993a, 1993b, 1995; Hofer *et al.* 1993; Sunquist & Sunquist 1996). Inevitably, most move into, or nearer to, zone 2. By assuming that the carnivores resident in zone 3 prey on herbivores in zone 2, this not only includes a realistic aspect of the Serengeti dynamics, but also prevents the Grant's gazelle population, in zone 3, from being seriously over-exploited. Consequently, this population is added to the Grant's gazelle population in zone 2 and the total number killed by carnivores is equally divided between the two populations.

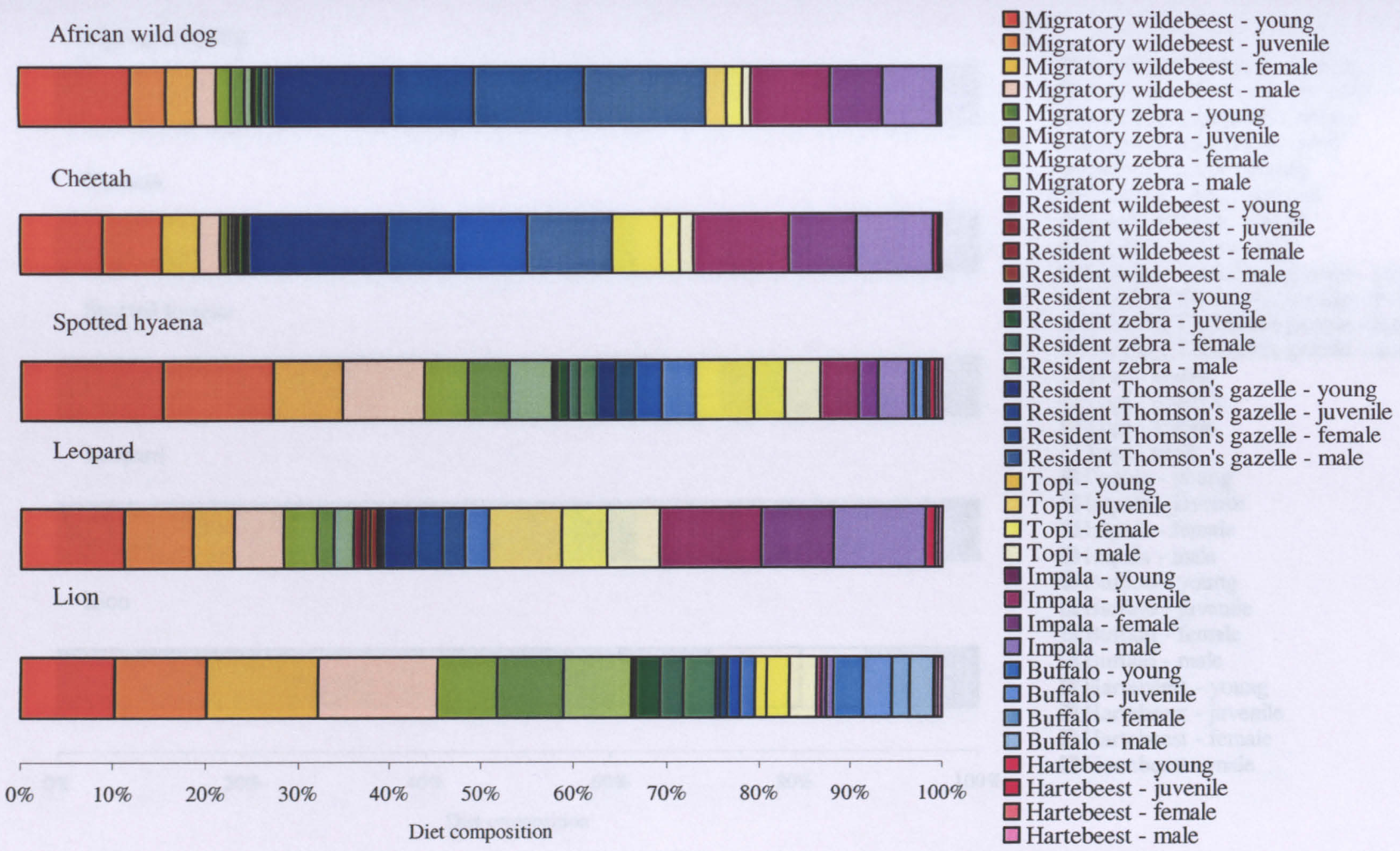

Figure 7.3 Diet composition of the five large carnivore components in zone 1 during the dry season.

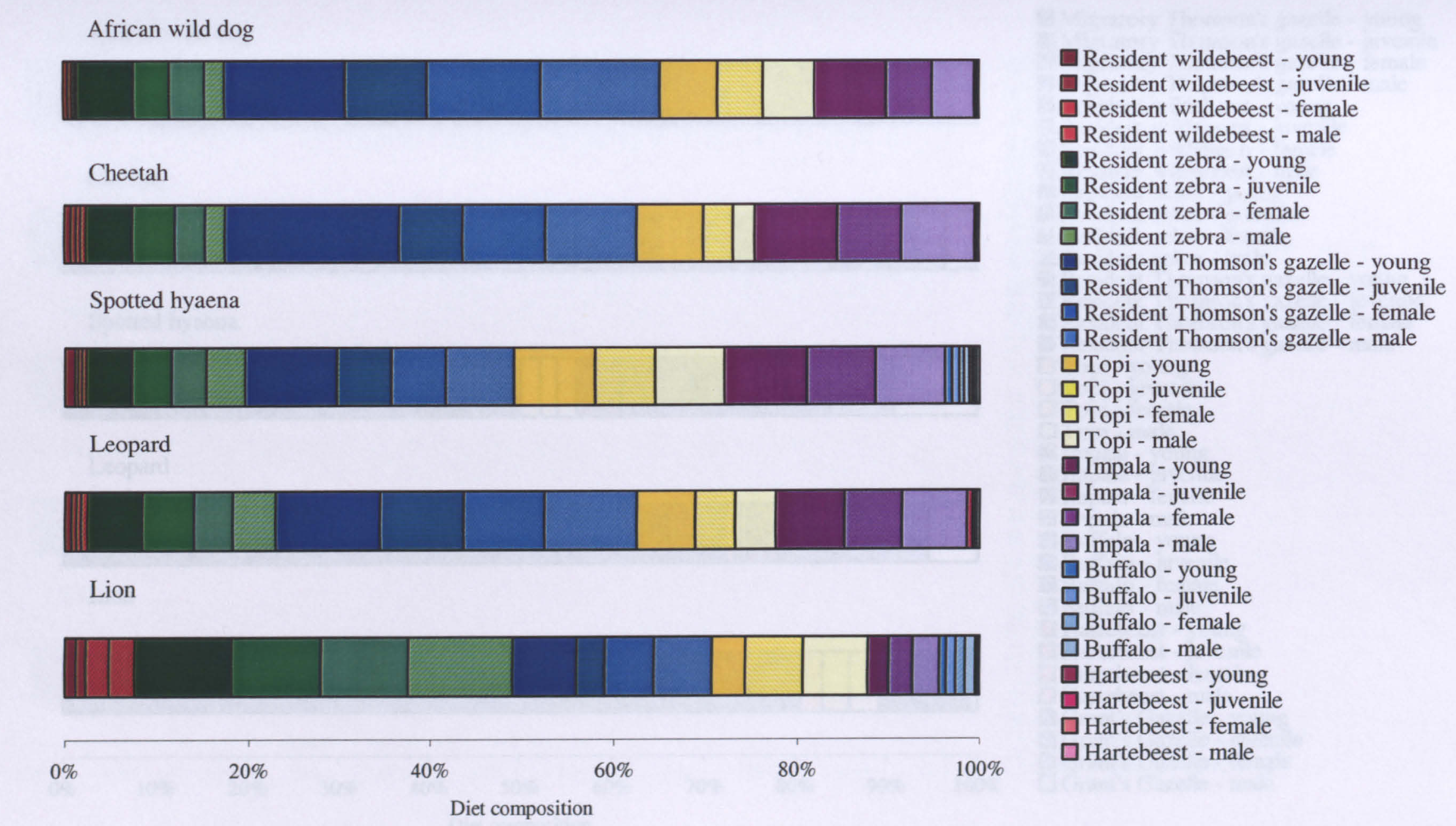

Figure 7.4 Diet composition of the five large carnivore components in zone 1 during the wet season.

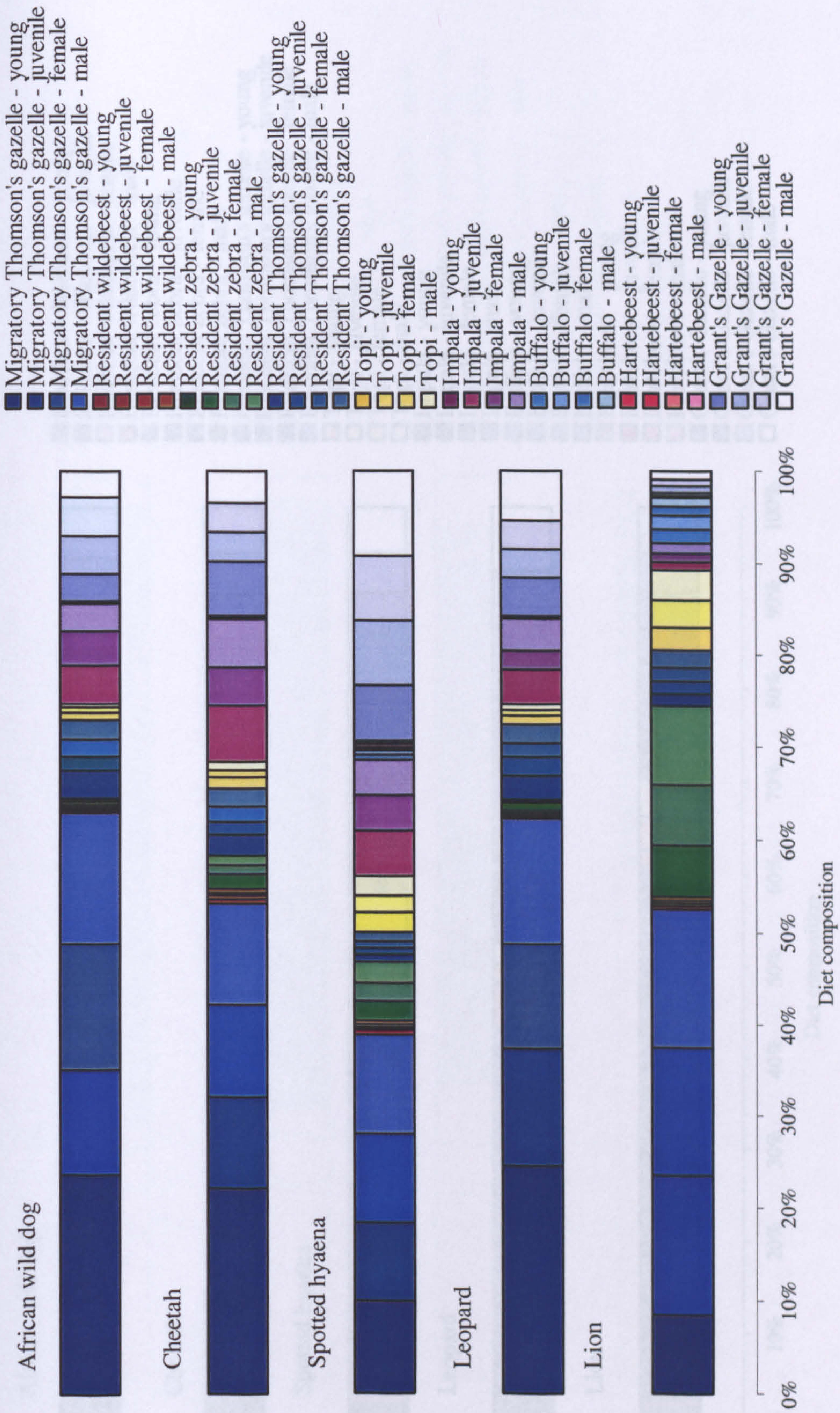

Figure 7.5 Diet composition of the five large carnivore components in zone 2 during the dry season.

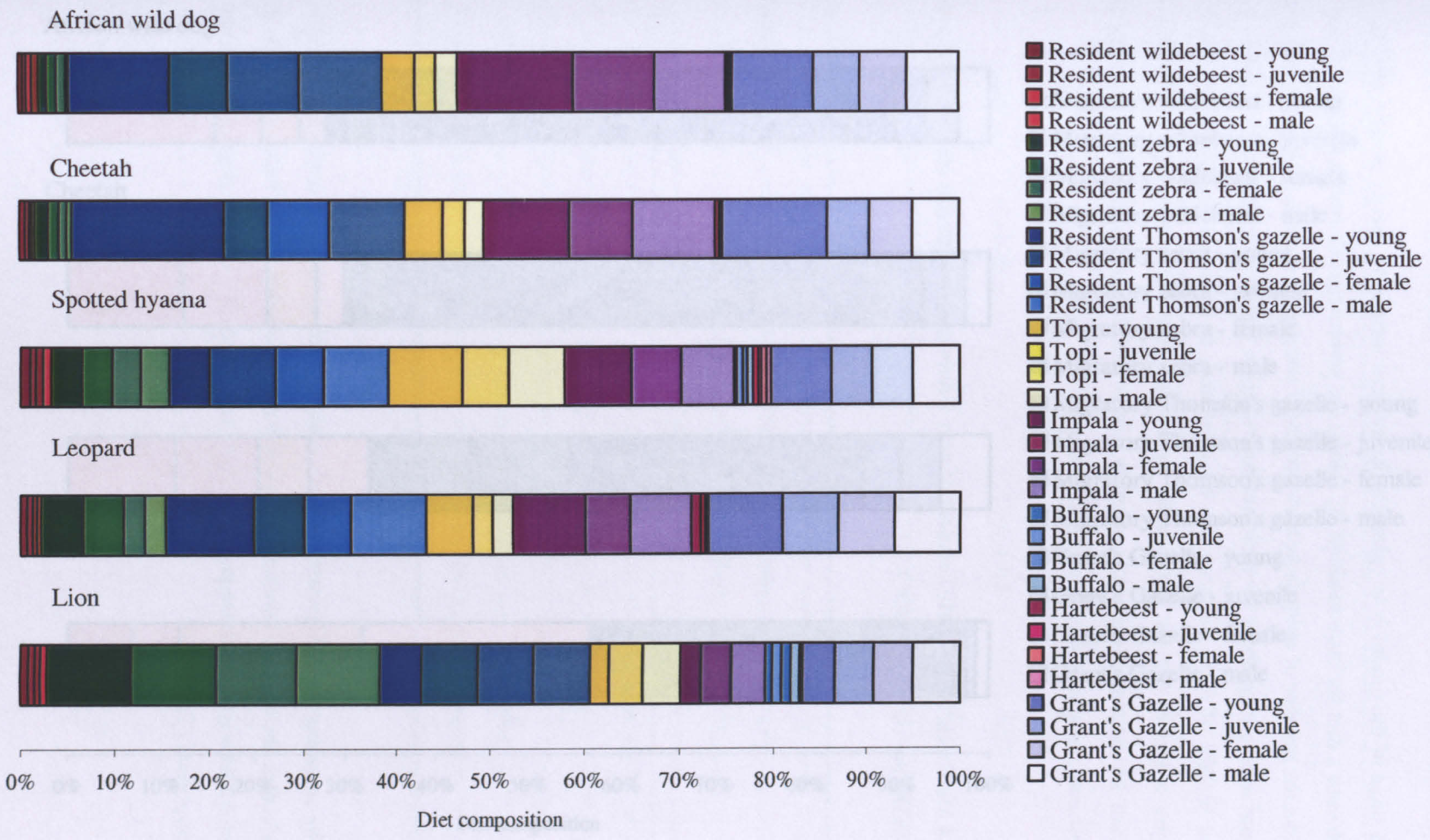

Figure 7.6 Diet composition of the five large carnivore components in zone 2 during the wet season.

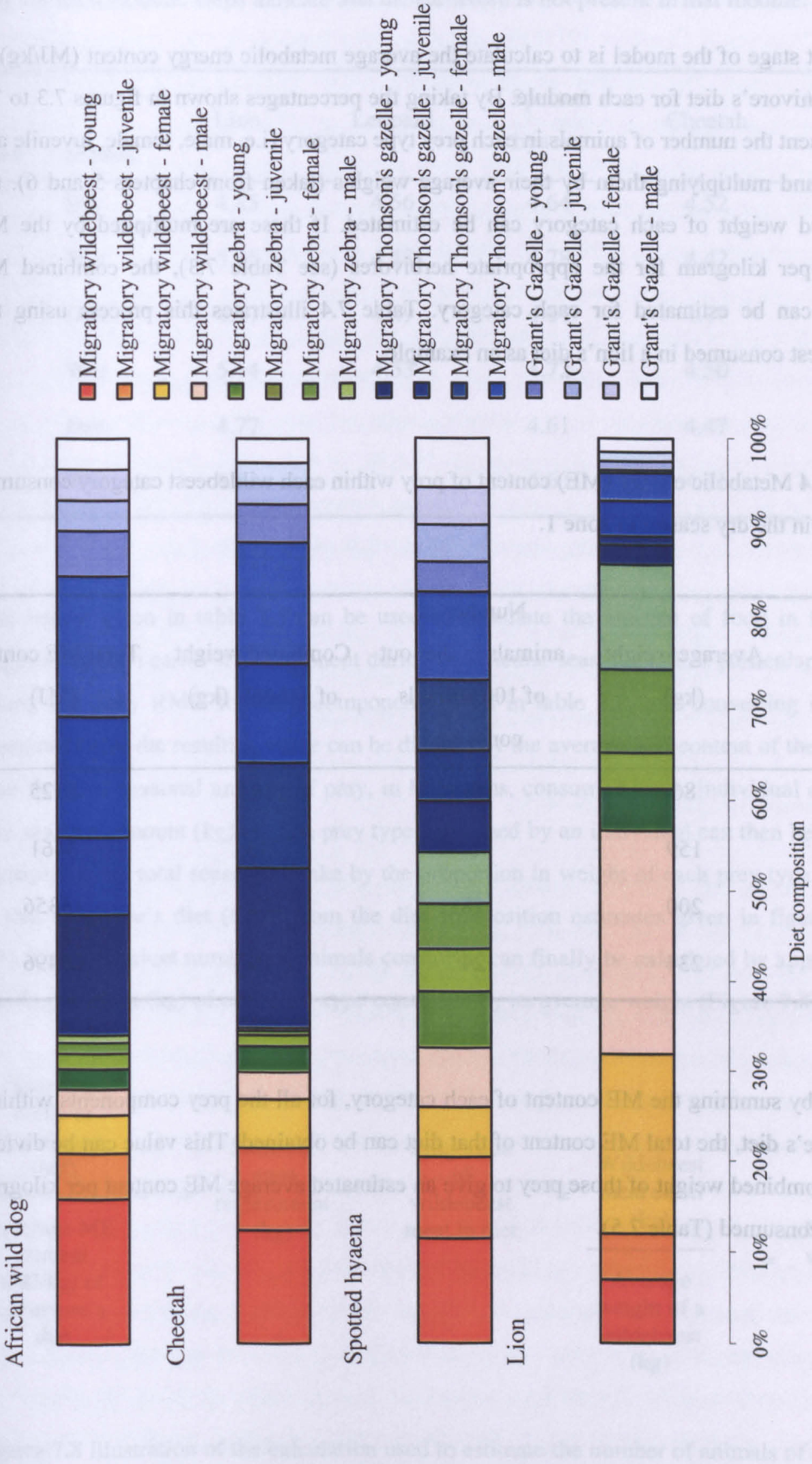

Figure 7.7 Diet composition of the five large carnivore components in zone 3 during the wet season.

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7.2.3 Seasonal herbivore consumption by individual carnivores

The next stage of the model is to calculate the average metabolic energy content (MJ/kg) of each carnivore's diet for each module. By taking the percentages shown in figures 7.3 to 7.7 to represent the number of animals in each prey type category (i.e. male, female, juvenile and young) and multiplying them by their average weights (taken from chapters 5 and 6), the combined weight of each category can be estimated. If these are multiplied by the ME content per kilogram for the appropriate herbivores (see Table 7.3), the combined ME content can be estimated for each category. Table 7.4 illustrates this process using the wildebeest consumed in a lion's diet as an example.

Table 7.4 Metabolic energy (ME) content of prey within each wildebeest category consumed by lions in the dry season in zone 1.

	Average weight (kg)	Number of animals in diet out of 100 animals consumed	Combined weight of animals (kg)	Total ME content (MJ)
Young	86	13	1103	5125
Juvenile	159	5	745	3461
Female	200	18	3520	16356
Male	234	24	5487	25496

Finally, by summing the ME content of each category, for all the prey components within a carnivore's diet, the total ME content of that diet can be obtained. This value can be divided by the combined weight of those prey to give an estimated average ME content per kilogram of prey consumed (Table 7.5).

Table 7.5 Average metabolic energy (ME) content (MJ/kg) of each carnivore component's diet for each module. Gaps indicate that the carnivore is not present in that module.

Zone	Season	Lion	Leopard	Spotted hyaena	Cheetah	African wild dog
1	Dry	4.85	4.56	4.64	4.52	4.54
	Wet	5.25	4.48	4.78	4.42	4.44
2	Dry	4.77	4.49	4.61	4.47	4.44
	Wet	5.14	4.53	4.72	4.50	4.49
3	Dry	4.77		4.61	4.47	4.44
	Wet	4.64		4.63	4.61	4.60

The values given in table 7.5 can be used to calculate the amount of food in kilograms required by each carnivore component during a particular season and in a particular zone. By taking the daily RMR for each component, given in table 7.2, and converting it to total seasonal RMR, the resulting value can be divided by the average ME content of their prey to give the total seasonal amount of prey, in kilograms, consumed by an individual carnivore. The seasonal amount (kg) of each prey type consumed by an individual can then be found by multiplying the total seasonal intake by the proportion in weight of each prey type featuring in that carnivore's diet (taken from the diet composition estimates given in figures 7.3 to 7.7). The equivalent number of animals consumed can finally be calculated by appropriately dividing amount (kg) of each prey type consumed by its average weight (Figure 7.8).

$$\frac{\text{Seasonal RMR of carnivore (MJ)}}{\text{Average ME content (MJ/kg) of carnivore's diet}} = \text{Seasonal meat requirement (kg)} \times \text{Proportion of wildebeest meat in diet} = \frac{\text{Wildebeest meat eaten (kg)}}{\text{Average weight of a wildebeest (kg)}} = \text{Number of wildebeest eaten}$$

Figure 7.8 Illustration of the calculation used to estimate the number of animals of each prey type (e.g. wildebeest) consumed by a individual carnivore over the period of a season.

However, a carnivore may kill an individual prey animal, but it may not eat all of it (Greenwood 1984). In other words, not all of a prey animal is edible (Briand Petersen & Casebeer 1971). Furthermore, what is edible to one carnivore may not be edible to another. For example, all the predators, except spotted hyaena, will not consume the skeleton, horns, skin and ears of a prey item (Ledger 1968; Mundy *et al.* 1983). Spotted hyaenas, on the other hand, not only have specially adapted bone-crushing teeth for splintering and grinding up the largest bones of wildebeest and zebra, but they are also adapted to digest them (Sutcliffe 1970; Kruuk 1972; Mills & Hofer 1998). Consequently, the proportion of a prey item available to a specific carnivore is dependent on those parts of a carcass that are edible to it. Blumenschine & Caro (1986) measured the four main carcass constituents, viscera, bone, skin and flesh, in a number of different ungulate species and found that their percentages were relatively similar not only between different species, but also between different functional groups (at 19.6 %, 24.8 %, 6.6 % and 49 % respectively). According to these percentages, spotted hyaenas consume 100 % of their kills, whilst the other four carnivore components consume only 68.6 % of their kills. If the average weight of each prey category is adjusted to represent the average amount of food available on a carcass, a more appropriate estimate of the number of animals killed by a carnivore can be made. The total number of individuals in each carnivore component can then be used to estimate the total number of prey types killed in each module.

7.2.4 Seasonal population numbers

Unfortunately, the Serengeti Research Institute only initiated large carnivore research projects in the mid-1960s, and prior to this, most research focused on the larger ungulate populations (Kruuk 1966b, 1969, 1972; Schaller 1972). Consequently, carnivore population numbers before this time are only speculative (Kruuk & Turner 1967). Furthermore, even from the mid-1960s carnivore population censuses have not been taken with any regularity for a number of reasons (Borner *et al.* 1987). It became obvious that those methods used for carrying out ungulate population censuses, such as aerial photography and counts from the ground, were unsuitable for carnivores (Grzimek & Grzimek 1960, Turner & Watson 1965a; Watson 1967; Kruuk 1972). This is because all five large carnivores seek shelter when not hunting, especially during the day. Spotted hyaenas and African wild dogs both have dens, while lions, leopards and cheetahs all rely to varying extents on vegetation for cover. Moreover, when these carnivores are out in the open they are so well camouflaged that it makes observation difficult even for a trained eye. One exception to this is the African wild dog, whose marbled coat pattern is thought to assist individual recognition in order to maintain social cohesion or at least help coordinate hunts by keeping all members of a pack in visual contact (Schaller 1972; Kingdon 1977). However, the ability to count dogs on a hunt does not constitute a population census, especially when members of the pack may remain behind at their den (Schaller 1972; Kingdon 1977).

Furthermore, the level of visibility varies between the different habitat types across the Serengeti. For instance, carnivores on the open plains may be more easily identified in comparison to those in the bush or open woodland (Kruuk 1972; Borner *et al.* 1987). Such reductions in visibility increase observational error, which in turn leads to a population underestimate (Kruuk 1972; Schaller 1972; Caro 1994). For example, the leopard's preference for dense woodland has proven particularly problematic when conducting a population survey (Schaller 1972; Nowell & Jackson 1996). In order to overcome such issues, mark-release-recapture techniques can be used to estimate population numbers (Kruuk & Turner 1967; Kruuk 1972). However, in large carnivores, the capture and handling of individuals is a time consuming and costly process (Kruuk 1972; Schaller 1972; Caro 1994). As a result, such studies are limited and sporadic, although since 1966, a number of lions and spotted hyaenas have been tagged (Kruuk & Turner 1967; Kruuk 1972; Schaller 1972). An alternative has been the creation of an archive of photographs identifying individual African wild dogs and cheetahs (Frame *et al.* 1979; Caro & Collins 1986; Caro 1994). From these studies, population estimates or censuses have been taken for each carnivore periodically in 1967, May 1977 and May 1986 for the whole of the Serengeti (Borner *et al.* 1987; Murray *et al.* 1992). These show that lion populations within the ecosystem increased rapidly during the 1970s and continued to increase although more slowly during the 1980s (Schaller 1972; Hanby & Bygott 1979; Borner *et al.* 1987; Murray *et al.* 1992). It is believed that this increase, and a similar increase in spotted hyaenas, coincided with the removal of rinderpest and subsequent rise in wildebeest and buffalo numbers (Murray *et al.* 1992; Durant 1998). In contrast, wild dogs have decreased rapidly in numbers since the 1960s, while cheetah populations have shown a relatively mild decrease (Schaller 1972; Borner *et al.* 1987; Caro & Collins 1986; Kat 1989). Although there is considerable speculation over the extent to which certain factors have influenced this decrease, one principal cause in both carnivores appears to be interference by their more abundant counterparts (Fanshawe *et al.* 1991; Gascoyne *et al.* 1993; Alexander & Appel 1994; Laurenson 1994, Laurenson 1995; Creel & Creel 1996; Kat *et al.* 1996; Carbone *et al.* 1997; Kelly *et al.* 1998; Vucetich & Creel 1999; Woodroffe & Ginsberg 1999; Durant 2000; Creel 2001; Scott & Scott 2001). Both cheetahs and wild dogs are vulnerable to kleptoparasitism and can easily lose their kills to lions and hyaenas (Caro 1994; Laurenson 1995; Creel & Creel 1996; Carbone *et al.* 1997; Gorman *et al.* 1998; Creel 2001). Consequently, the increase in the latter two species has amplified their competitive pressure to the extent that they may suppress or decrease cheetah and wild dog numbers (Kat 1989; Kelly *et al.* 1998).

In contrast, investigations into leopard numbers in the Serengeti during this period have suggested that they have remained relatively constant. Unlike the other carnivores, population estimates for leopard were based on their density within the region (Schaller 1972; Bertram 1982; Bourlière 1983). For these, Schaller (1972) identified that leopards in Seronera (zone 2) had permanent ranges, which they retained for a considerable part of their lives. As a result, he was able to distinguish the range size of several leopards through sightings over a number of years. This study revealed that ranges were about 40 to 60 km^2, female ranges were smaller and there was varying degrees of overlap. A corresponding study in Wilpattu National Park by Eisenberg (1970) confirmed that there was little overlap, if any, between same sex ranges, although male ranges generally overlapped a number of female ranges. Consequently, Schaller (1972) was able to estimate the number of leopards in the area by assuming an average density based on his and Eisenberg's findings. A further study by Bertram (1978, 1982), which involved radio tracking leopards in the northern woodlands of the Serengeti (zone 1), revealed that ranges there were much smaller in comparison, at approximately 15 to 20 km^2. This was thought to be an indication of the quality of the habitat in that area and this in turn influenced the number of leopards there (Borner *et al.* 1987; Mizutani & Jewell 1998). Continued observations suggest that leopard populations have remained fairly constant throughout the Serengeti. This may not be surprising since they endure the least competitive pressure from other carnivores and are unlikely to benefit from larger numbers of wildebeest and buffalo (Kingdon 1977).

Table 7.6 is a compilation of all the population data available for the five carnivore components. Although it presents rather general figures for the 60s, 70s, and 80s, at this stage in the model it was thought that no more detail than this was required. (Kruuk & Turner 1967; Stewart & Talbot 1962; Talbot & Talbot 1963; Adamson 1964; Kruuk 1969, 1972; Schaller 1972; Frame *et al.* 1979; Gittleman & Harvey 1982; Caro & Collins 1986; Ammann 1987; Borner *et al.* 1987; Durant *et al.* 1988; Kat 1989; Caro 1994; Burrows *et al.* 1994; Burrows 1995; Caro & Durant 1995; Ginsberg *et al.* 1995; Hanby *et al.* 1995; Creel & Creel 1996; Woodroffe *et al.* 1997; Durant 1998; Mills & Hofer 1998; Woodroffe & Ginsberg 1999; Scott & Scott 2001; Ogutu & Dublin 2002).

Table 7.6 Population numbers for each carnivore component in the various zones of the Serengeti over the 1960s,1970s and 1980's.

		Predator numbers		
	Carnivore	Zone 1	Zone 2	Zone 3
1960s	Lion	1050	1000	150
	Cheetah	86	106	410
	Leopard	490	360	0
	Hunting dog	85	106	94
	Spotted hyaena	399	498	2100
1970s	Lion	1439	1370	206
	Cheetah	69	93	380
	Leopard	490	360	0
	Hunting dog	37	47	41
	Spotted hyaena	411	520	3393
1980s	Lion	1754	1670	251
	Cheetah	55	76	334
	Leopard	490	360	0
	Hunting dog	14	17	15
	Spotted hyaena	426	534	4261

7.3 TOTAL EFFECT OF PREDATION

The population numbers of each carnivore component in each zone, given in table 7.6, can be applied to the equivalent seasonal intake for an individual carnivore to establish the overall number of prey types eaten by each component, in a particular module, during each decade. Furthermore, if the number of prey consumed by each component is combined, the total number of prey types consumed by predators is attained. Figures 7.9 to 7.13 illustrate these overall estimated figures for each module. A figure for zone 3 is not included as the dry season population numbers for this module are combined with those for zone 2 (refer back to section 7.2.2.6).

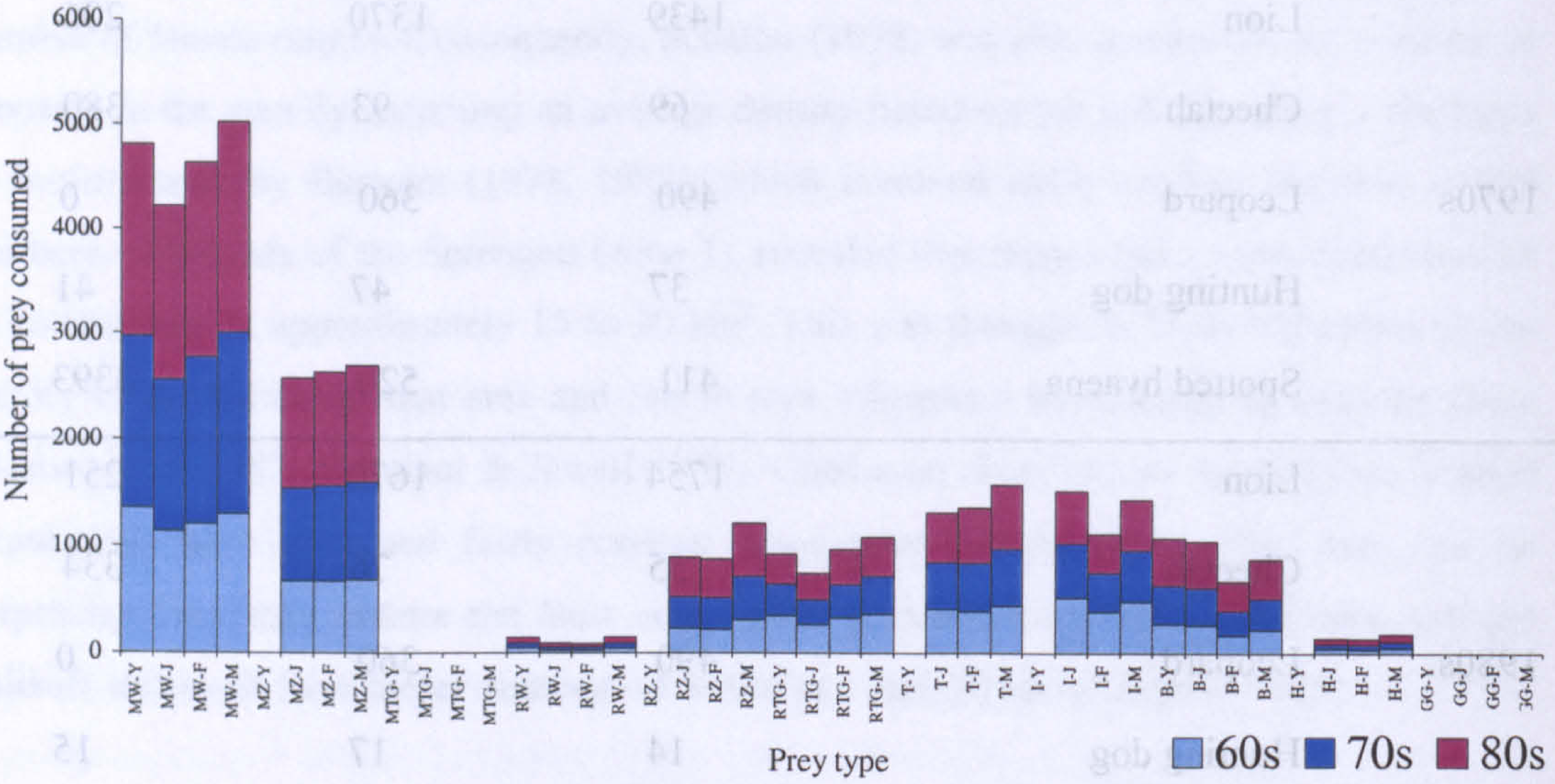

Figure 7.9 Estimated number of prey consumed by carnivores in zone 1 during the dry season for 1960s, 1970s and 1980s. See figures 7.3-7.7 for key to prey types.

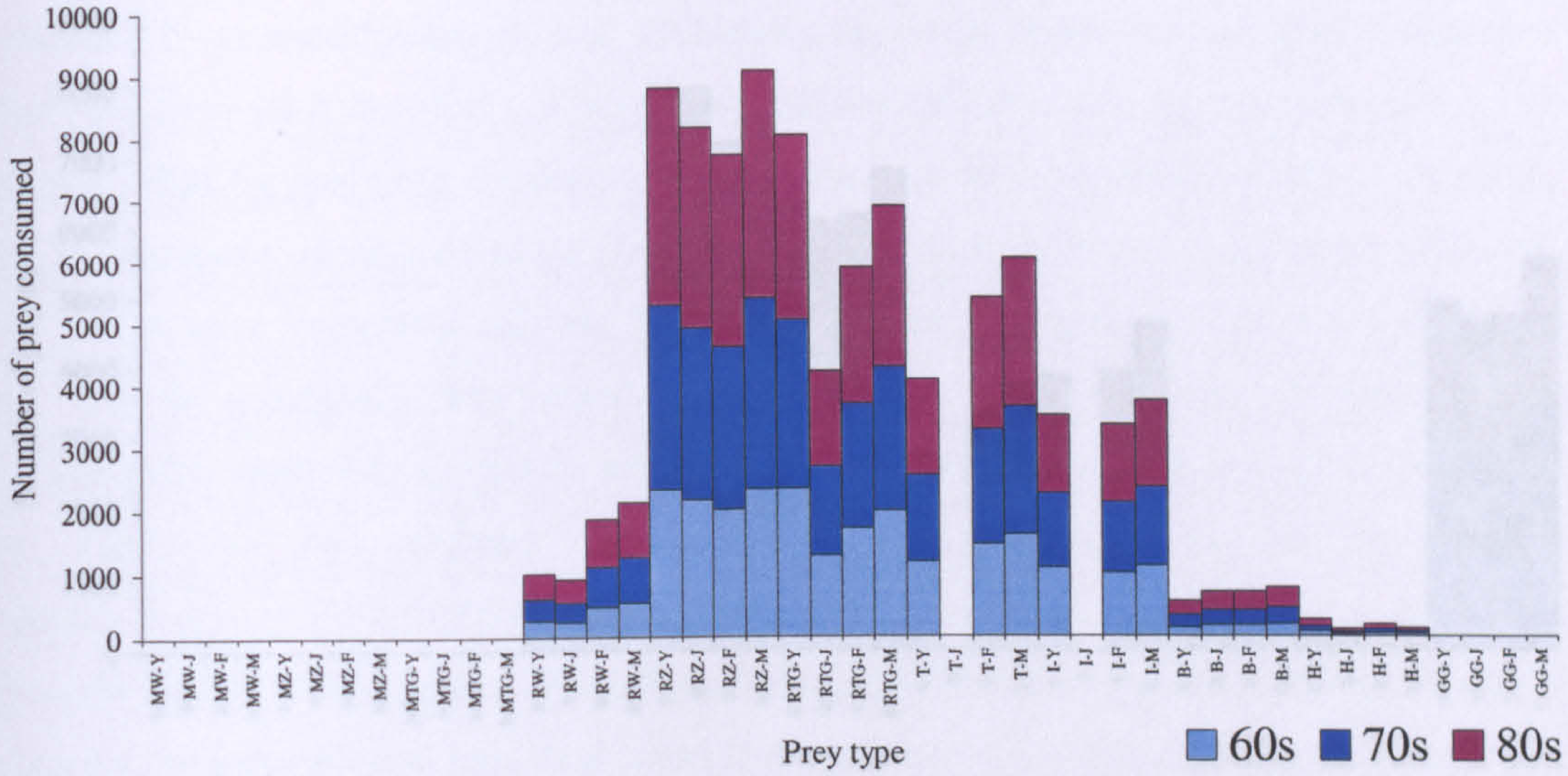

Figure 7.10 Estimated number of prey consumed by carnivores in zone 1 during the wet season for 1960s, 1970s and 1980s. See figures 7.3-7.7 for key to prey types.

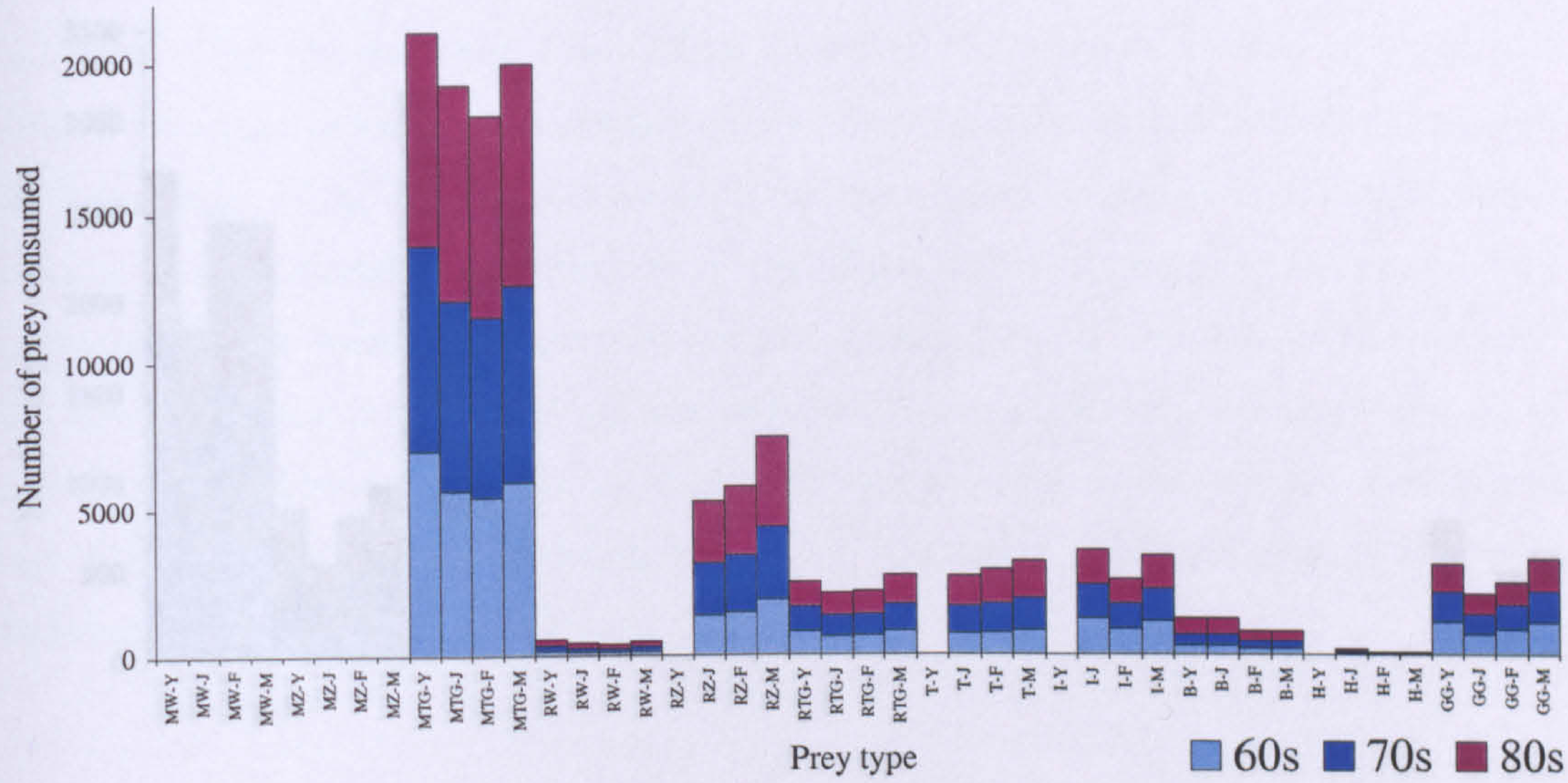

Figure 7.11 Estimated number of prey consumed by carnivores in zone 2 during the dry season for 1960s, 1970s and 1980s. See figures 7.3-7.7 for key to prey types.

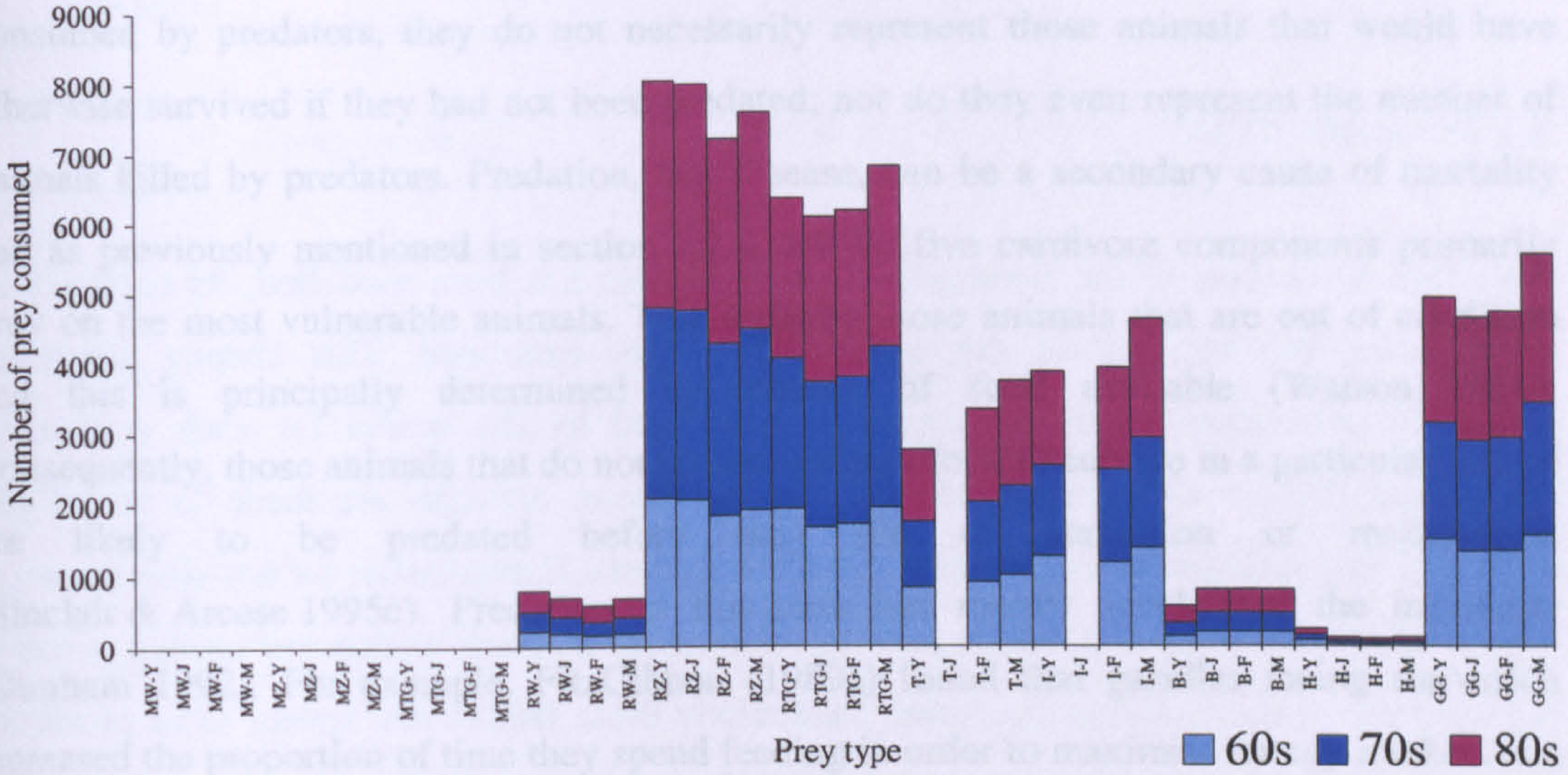

Figure 7.12 Estimated number of prey consumed by carnivores in zone 2 during the wet season for 1960s, 1970s and 1980s. See figures 7.3-7.7 for key to prey types.

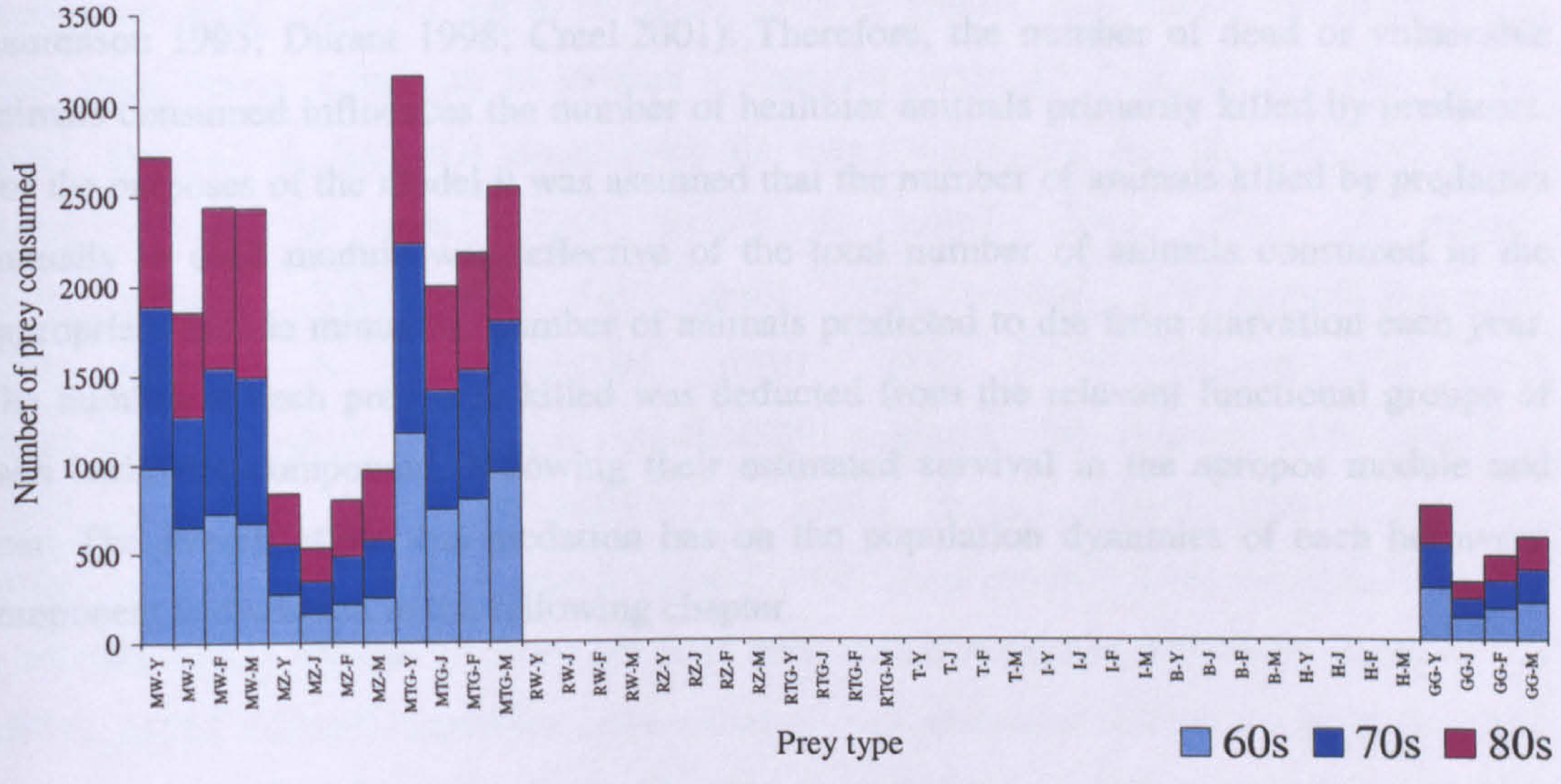

Figure 7.13 Estimated number of prey consumed by carnivores in zone 3 during the wet season for 1960s, 1970s and 1980s. See figures 7.3-7.7 for key to prey types.

Although the values illustrated in the previous figures represent the number of animals consumed by predators, they do not necessarily represent those animals that would have otherwise survived if they had not been predated, nor do they even represent the number of animals killed by predators. Predation, like disease, can be a secondary cause of mortality and as previously mentioned in section 7.2.4, all the five carnivore components primarily prey on the most vulnerable animals. This includes those animals that are out of condition and this is principally determined by amount of food available (Watson 1966). Consequently, those animals that do not receive enough food to survive in a particular season are likely to be predated before they die of starvation or malnutrition (Sinclair & Arcese 1995c). Predation in this case has merely accelerated the inevitable (Dunham 1992). For example, FitzGibbon (1989a) found that gazelles facing starvation increased the proportion of time they spend feeding in order to maximise energy intake. As a result, they were forced to reduce their vigilance and subsequently became more vulnerable to hunting by cheetahs. Furthermore, the diets of those carnivores that scavenge, such as lions, leopards and especially spotted hyaenas, is supplemented by animals that have succumbed to starvation and/or disease (Kruuk 1966a; Kruuk & Turner 1967; Houston 1979; Sinclair 1977B; Melton & Melton 1982; McNaughton & Georgiadis 1986; Henschel & Skinner 1990; Gasaway *et al.* 1991; Fanshawe & FitzGibbon 1993; Creel & Creel 1995; Laurenson 1995; Durant 1998; Creel 2001). Therefore, the number of dead or vulnerable animals consumed influences the number of healthier animals primarily killed by predators. For the purposes of the model it was assumed that the number of animals killed by predators annually in each module was reflective of the total number of animals consumed in the appropriate decade minus the number of animals predicted to die from starvation each year. The number of each prey type killed was deducted from the relevant functional groups of each herbivore component, following their estimated survival in the apropos module and year. The overall effect this predation has on the population dynamics of each herbivore component is discussed in the following chapter.

CHAPTER 8: TESTING THE MODEL.

8.1 INTRODUCTION

Now that a sub-unit of the Serengeti-Mara ecosystem has been modelled, its accuracy at representing this sub-unit of the ecosystem can be examined. This chapter compares estimated population numbers with those calculated by the model for each equivalent component. Where differences between the two occur, attempts are made to reveal the source of this variation using a series of sensitivity tests. Explanations for any discrepancies identified are discussed and, where possible, alternative methods or data are applied. Finally, the outcome of the model is discussed, particularly those factors that appear to be primarily regulating individual herbivore components, such as grass availability, predation and factors as yet not incorporated.

8.2 ESTIMATED POPULATION NUMBERS

In order to reveal whether annual population numbers for each herbivore component predicted by the model were similar to those observed in the Serengeti-Mara ecosystem, census data was required. However, although a number of population counts have been undertaken, they do not adequately cover all components (Grzimek & Grzimek 1960; Stewart & Talbot 1962; Talbot & Talbot 1963; Talbot & Stewart 1964; Watson & Kerfoot 1964; Watson 1965, 1966, 1967; Kruuk 1972; Schaller 1972; Braun 1973; Sinclair 1973a, 1974b, 1977b, 1979c; Delany & Happold 1979; Grimsdell 1979; Houston 1979; Kingdon 1982b; Borner *et al.* 1987; Rodgers & Swai 1988; Onyeanusi 1989; Dublin *et al.* 1990; Caro 1994; Campbell & Borner 1995; Campbell & Hofer 1995; Hilborn *et al.* 1995; Sinclair & Arcese 1995c; Mduma *et al.* 1999). For instance, only those components that have been the focus of detailed studies provide a relatively good source of census data, such as buffalo and wildebeest (Sinclair 1973a, 1974b, 1979c). Fortunately, only a general population trend is required to make a basic comparison between calculated numbers and estimated numbers. Consequently, wherever possible, SPSS was used to replace missing data with estimated linear values (SPSS 1998). For those components with very little available census data, and no written accounts to suggest a change in population numbers, it was assumed that their populations remained constant. This applied to resident wildebeest, zebra and Thomson's gazelle, and consequently their numbers were taken to be constant around those figures given in table 6.2. Figures 8.1 & 8.2 illustrate the population trends of the remaining components.

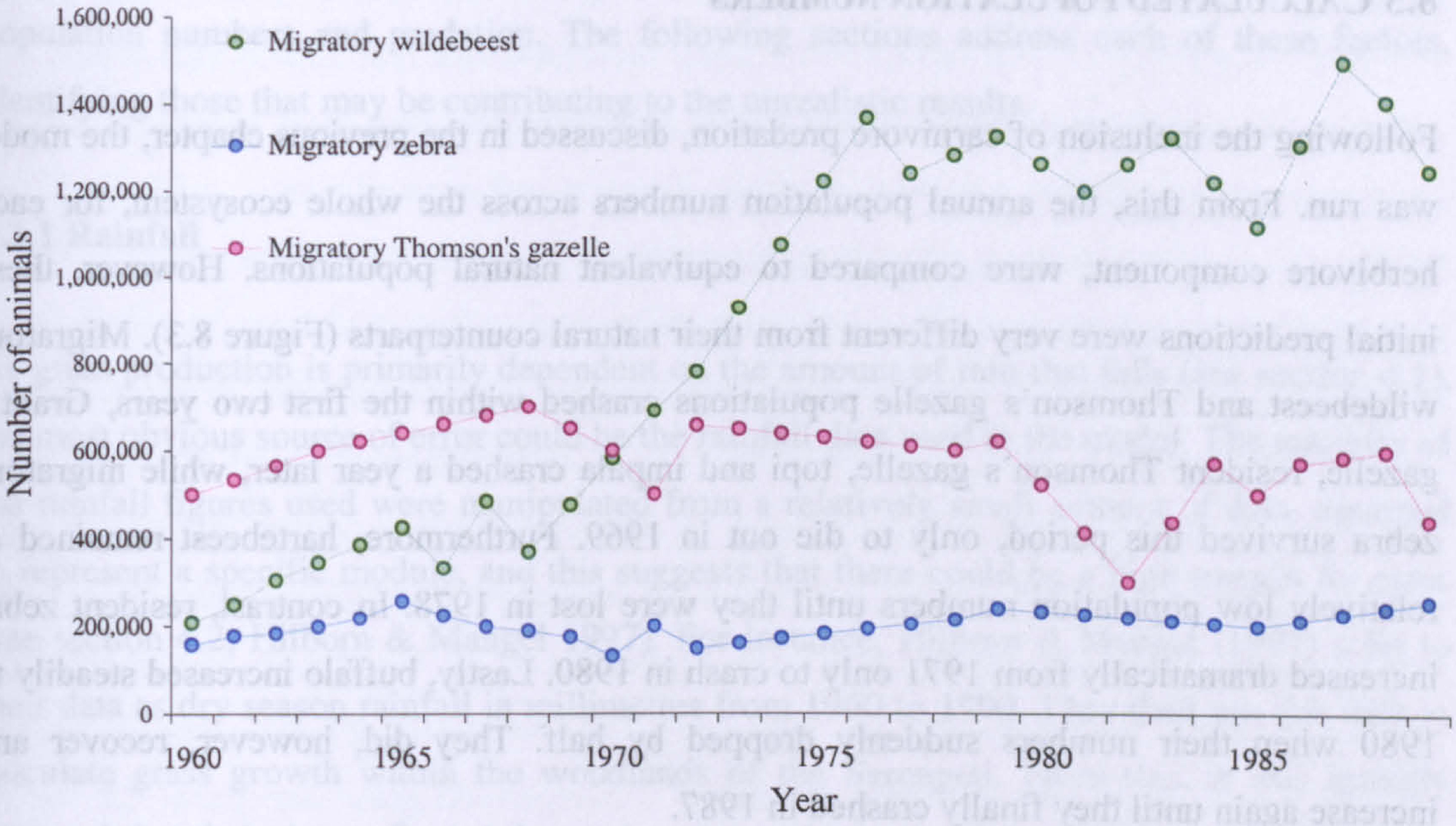

Figure 8.1 Estimated annual population values for migratory herbivore components manipulated from census data.

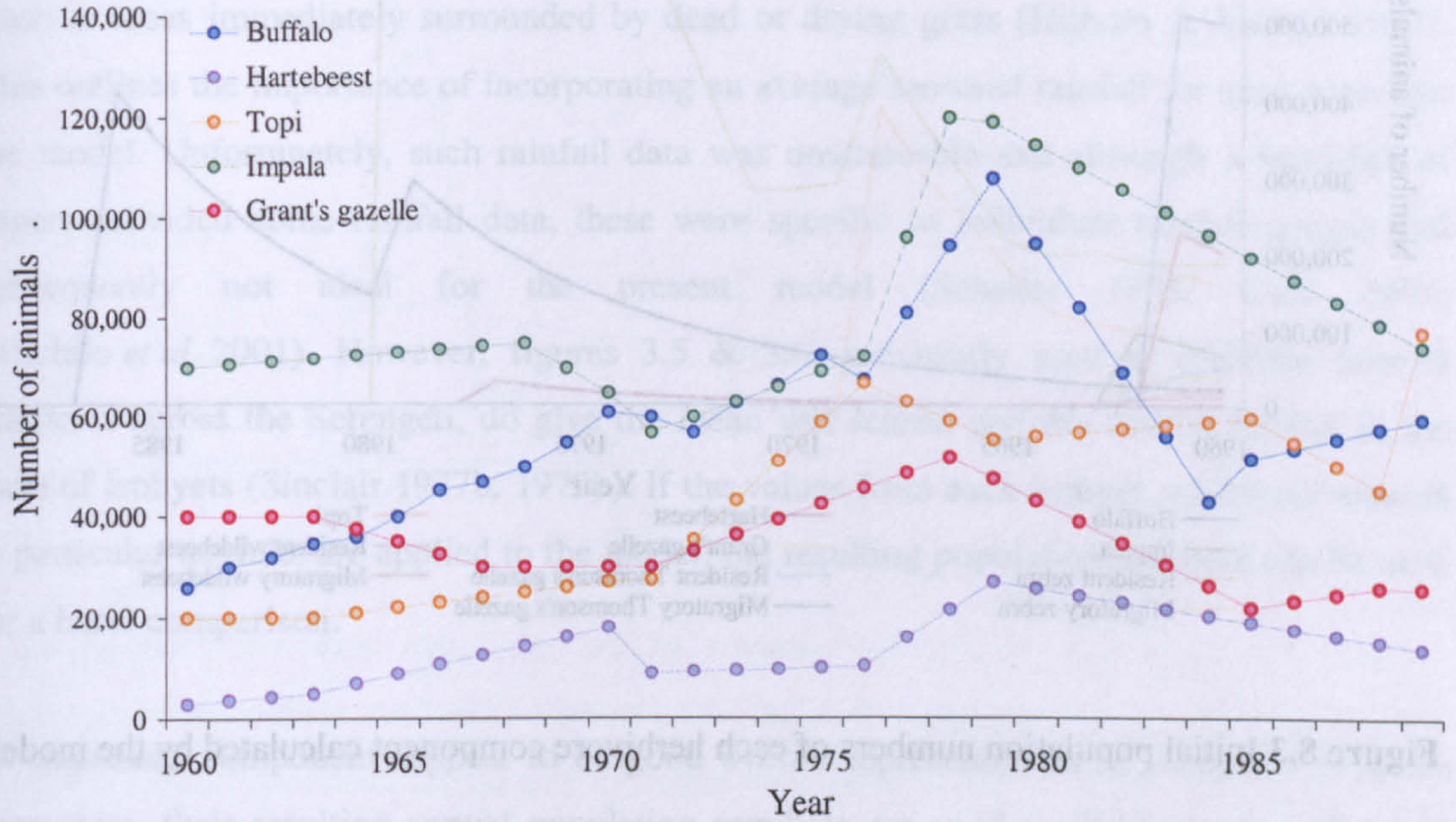

Figure 8.2 Estimated annual population values for resident herbivore components manipulated from census data.

8.3 CALCULATED POPULATION NUMBERS

Following the inclusion of carnivore predation, discussed in the previous chapter, the model was run. From this, the annual population numbers across the whole ecosystem, for each herbivore component, were compared to equivalent natural populations. However, these initial predictions were very different from their natural counterparts (Figure 8.3). Migratory wildebeest and Thomson's gazelle populations crashed within the first two years, Grant's gazelle, resident Thomson's gazelle, topi and impala crashed a year later, while migratory zebra survived this period, only to die out in 1969. Furthermore, hartebeest remained at relatively low population numbers until they were lost in 1978. In contrast, resident zebra increased dramatically from 1971 only to crash in 1980. Lastly, buffalo increased steadily to 1980 when their numbers suddenly dropped by half. They did, however, recover and increase again until they finally crashed in 1987.

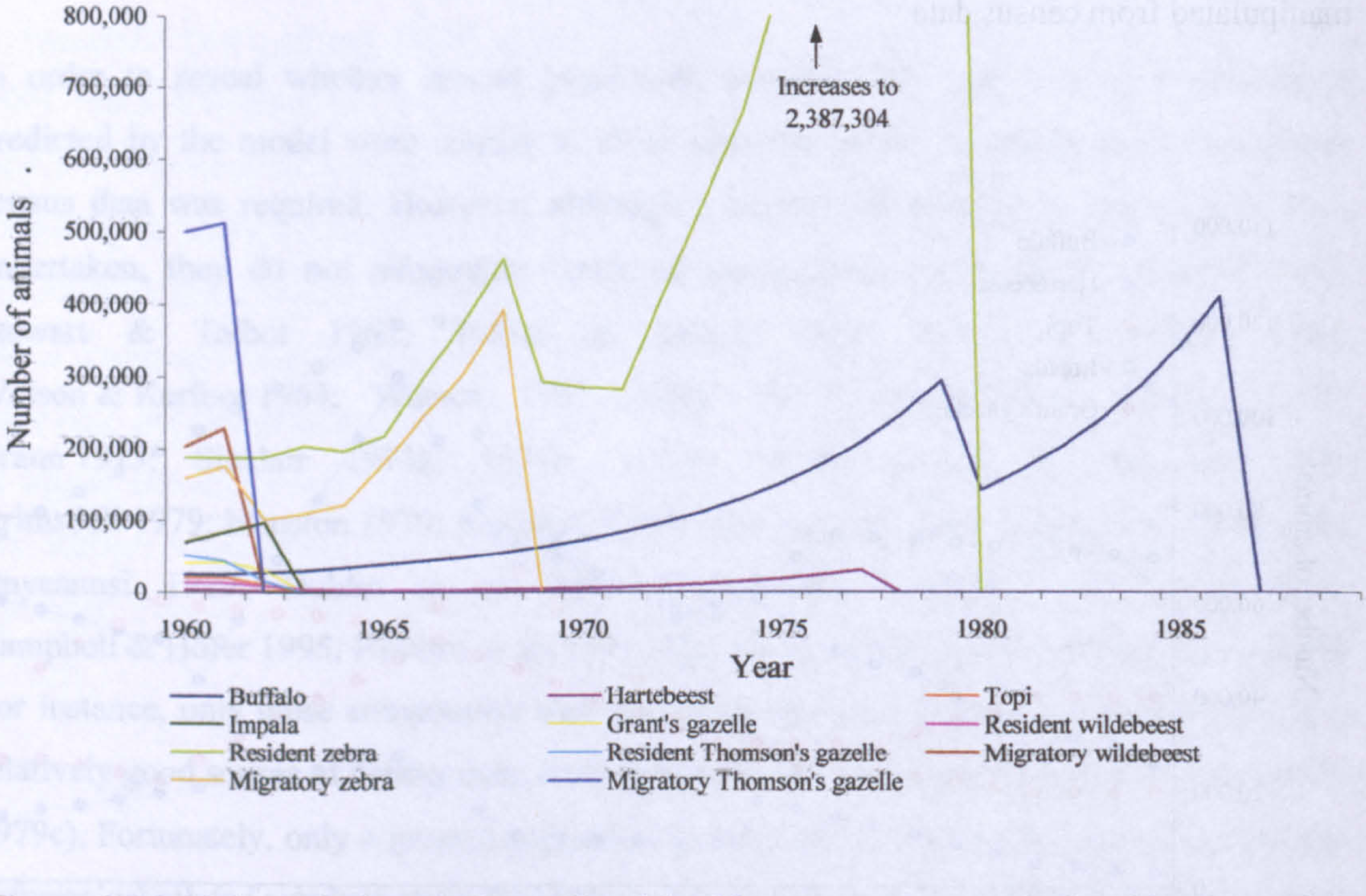

Figure 8.3 Initial population numbers of each herbivore component calculated by the model.

Although these initial results appear to be at odds with the field estimates, they indicate that the overall cause is a severe lack of green grass. For instance, even when buffalo are the only component left in 1980, they still crash six years later with a population only reaching 413,000. This underestimation in primary production in the model could be due to a number of reasons, including incorrect rainfall, grass growth, maturation, grazing, burning, population numbers and predation. The following sections address each of these factors, identifying those that may be contributing to the unrealistic results.

8.3.1 Rainfall

As grass production is primarily dependent on the amount of rain that falls (see section 4.1), the most obvious source of error could be the rainfall data used in the model. The majority of the rainfall figures used were manipulated from a relatively small amount of data, assumed to represent a specific module, and this suggests that there could be a high margin for error (see section 4.2; Hilborn & Mangel 1997). For instance, Hilborn & Mangel (1997) refer to their data as dry season rainfall in millimetres from 1960 to 1990. They then use this data to calculate grass growth within the woodlands of the Serengeti. From this, it was initially assumed that their data reflected the total amount of rain that fell during each dry season in the north, therefore zone 1. Furthermore, Hilborn & Mangel (1997) fail to indicate whether this data was collected from an individual rain gauge, or a number of gauges in the area. Again, it can only be assumed that the latter is applicable, particularly as Hilborn & Mangel, in the same paper, recognise that almost all rain falls in patchy thundershowers. This patchiness is particularly noticeable in the dry season when localised showers cause a green flush in areas immediately surrounded by dead or drying grass (Hilborn & Mangel 1997). This outlines the importance of incorporating an average seasonal rainfall for each zone into the model. Unfortunately, such rainfall data was unattainable and although a hand-full of papers provided some rainfall data, these were specific to individual rainfall gauges and subsequently not ideal for the present model (Schaller 1972; Caro 1994; Ottichilo *et al.* 2001). However, figures 3.5 & 3.6, previously used to illustrate rainfall gradients across the Serengeti, do give the mean wet season and dry season rainfall in the form of isohyets (Sinclair 1977b, 1979b). If the values from each isohyet, which correspond to particular module, are applied to the model, the resulting population numbers can be used for a basic comparison.

As migratory components appear to be good overall representatives of components in the ecosystem, their resulting annual population numbers are used to illustrate the effects of applying the isohyet values to the model (Figure 8.4). They reveal that the amount of grass available increases considerably by simply using a mean seasonal rainfall of 300 mm, 200 mm and 100 mm in the dry season, and 700 mm, 600 mm and 500 mm in the wet season for zones 1, 2 and 3 respectively. Furthermore, those component populations that do die out, only do so when they, or other components, have increased to unnaturally high numbers.

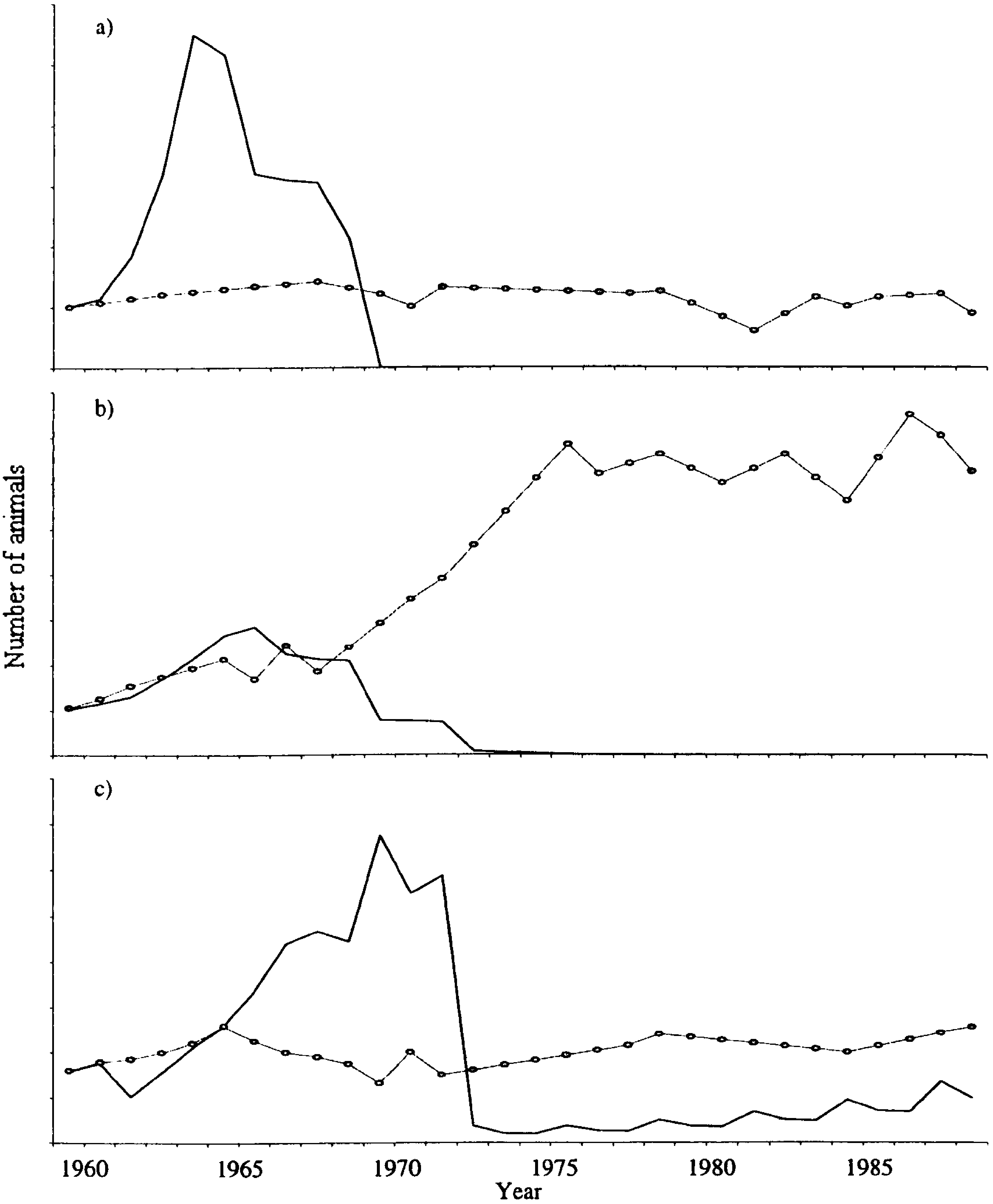

Figure 8.4 Estimated populations numbers of the migratory herbivore components, a) Thomson's gazelle, b) wildebeest c) zebra, when mean wet and dry season rainfall is applied to the model (Sinclair 1977b, 1979b). The solid line represents calculated numbers and the dotted line represents estimated population numbers.

There are a number of conceivable explanations for these high population numbers. Firstly, the model may predict that either survival rates, recruitment rates or both are much higher for the amount of green grass available than they would be in the wild. For recruitment rates to be too high, either the recruitment cycles used are incorrect (see Figures 5.16, 6.1 and 6.3-6.8), predicting that an animal can produce more offspring than physiologically possible, or the costs of reproduction (i.e. conception and pregnancy) are too low. Considering the large number of investigations on the physiology and reproductive biology of each species used to create the recruitment cycles, it is unlikely that there are fundamental inaccuracies with the cycles applied to the model. On the other hand, Blaxter's (1989) metabolic data used to estimate the costs of reproduction for each herbivore species in the model may not be appropriate (see section 5.4.1). To test this, a sensitivity analysis was conducted, in which the metabolic costs of conception and pregnancy were increased at 50 % increments. Figure 8.5 illustrates, using the migratory Thomson's gazelle as an example, that even an increase of 200 % has little influence on the population numbers. This implies that unless Blaxter's figures are very inaccurate, departures from the reproductive costs of those herbivores in the wild are negligible to the population numbers predicted in the model.

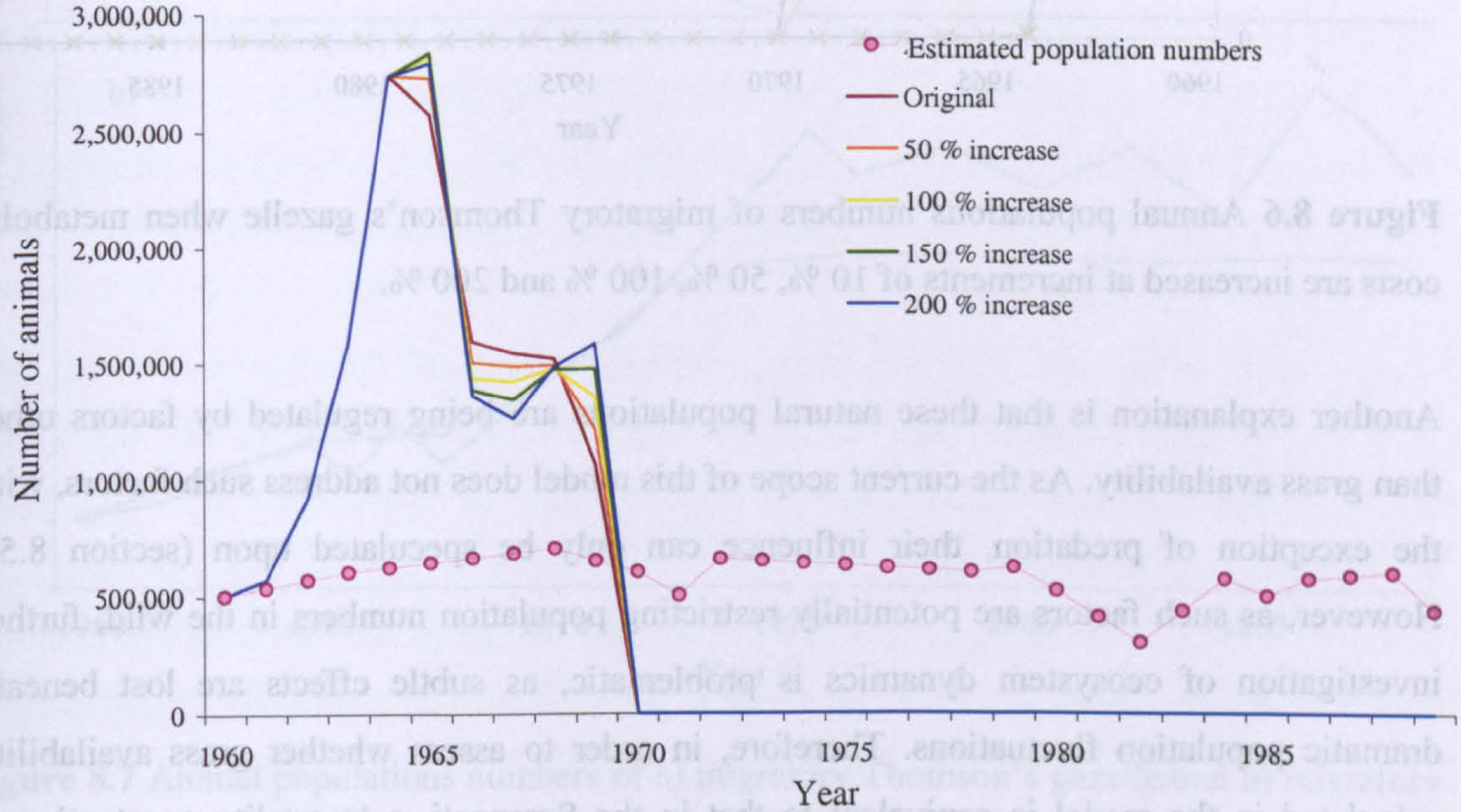

Figure 8.5 Annual populations numbers of migratory Thomson's gazelle when recruitment costs are increased at increments of 50 %.

Alternatively, low metabolic rates may be causing population numbers to exceed natural levels through increased survival. Once again, a sensitivity analysis was conducted to investigate this, in which the metabolic costs (RMRs, see section 5.3) were increased at increments of 10 %, 50 %, 100 % and 200 %. Figure 8.6 illustrates that although increasing RMRs by up to 50 % reduces survival rates initially, these numbers are still well above their natural equivalents, indicating that metabolic rates are not the causative factor.

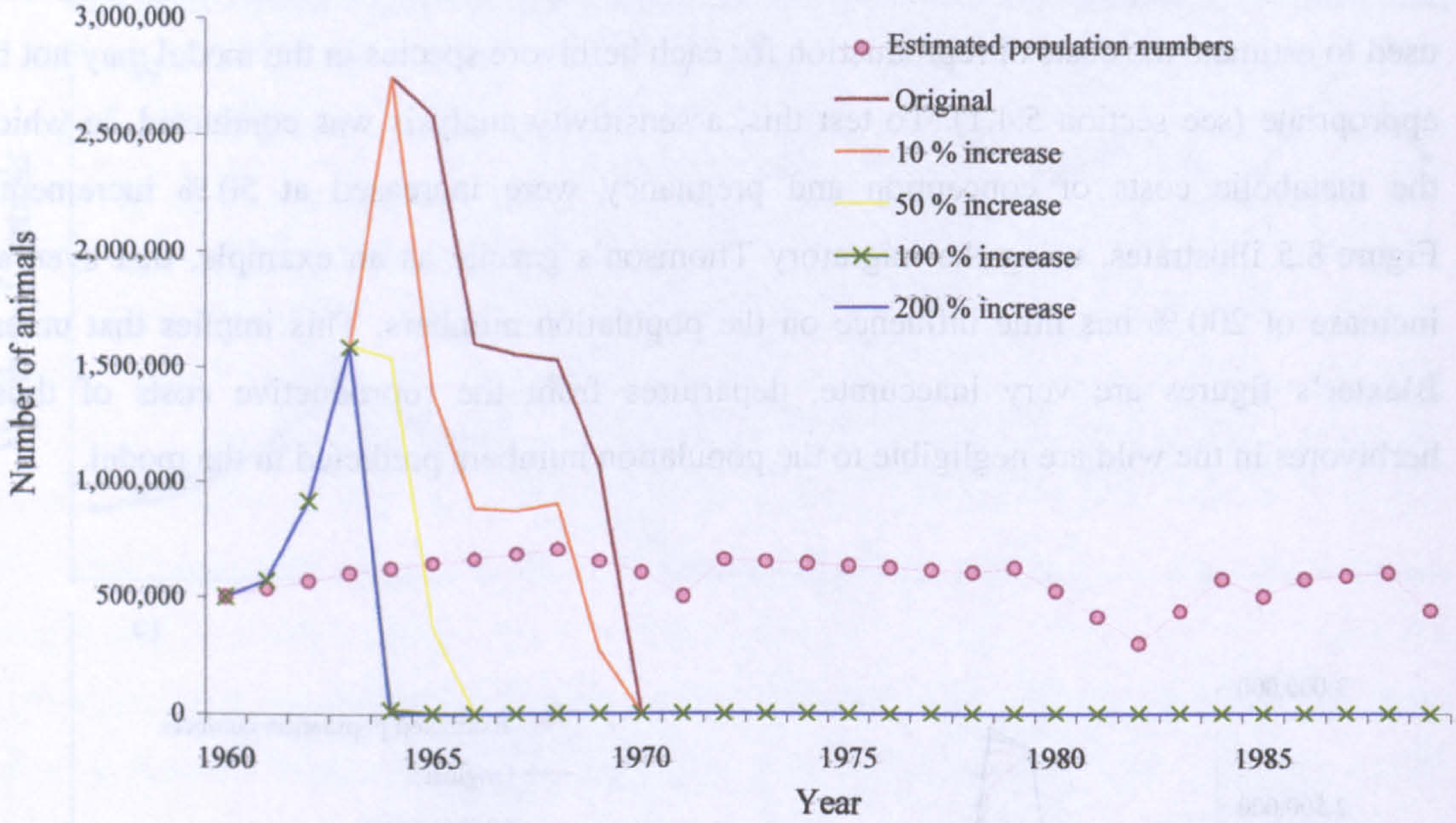

Figure 8.6 Annual populations numbers of migratory Thomson's gazelle when metabolic costs are increased at increments of 10 %, 50 %, 100 % and 200 %.

Another explanation is that these natural populations are being regulated by factors other than grass availability. As the current scope of this model does not address such factors, with the exception of predation, their influence can only be speculated upon (section 8.5). However, as such factors are potentially restricting population numbers in the wild, further investigation of ecosystem dynamics is problematic, as subtle effects are lost beneath dramatic population fluctuations. Therefore, in order to assess whether grass availability calculated in the model is equivalent to that in the Serengeti, a 'mortality constant' was introduced to restrict components from increasing dramatically above their natural levels and subsequently removing any interference from unnatural population fluctuations (Figure 8.7). For this, an annual mortality value was applied to each component, representing 1 % of the population. This value was then increased systemically until the population numbers of the component concerned attained a level comparable to its natural population.

Following this, it was found that under these limitations four components did not reach their natural population levels. The first was migratory Thomson's gazelle and, as illustrated in figure 8.7, their numbers suddenly dropped in 1971. On further investigation, it was found that this drop occurred specifically in zone 3 during the wet season. The lack of grass in this module was also responsible for restricting migratory wildebeest numbers below their natural levels (Figure 8.7) and causing a steady decrease in the Grant's gazelle population. Finally, resident Thomson's gazelle also diverged from their natural population, primarily as a result of limited grass availability in zone 1 during the dry season.

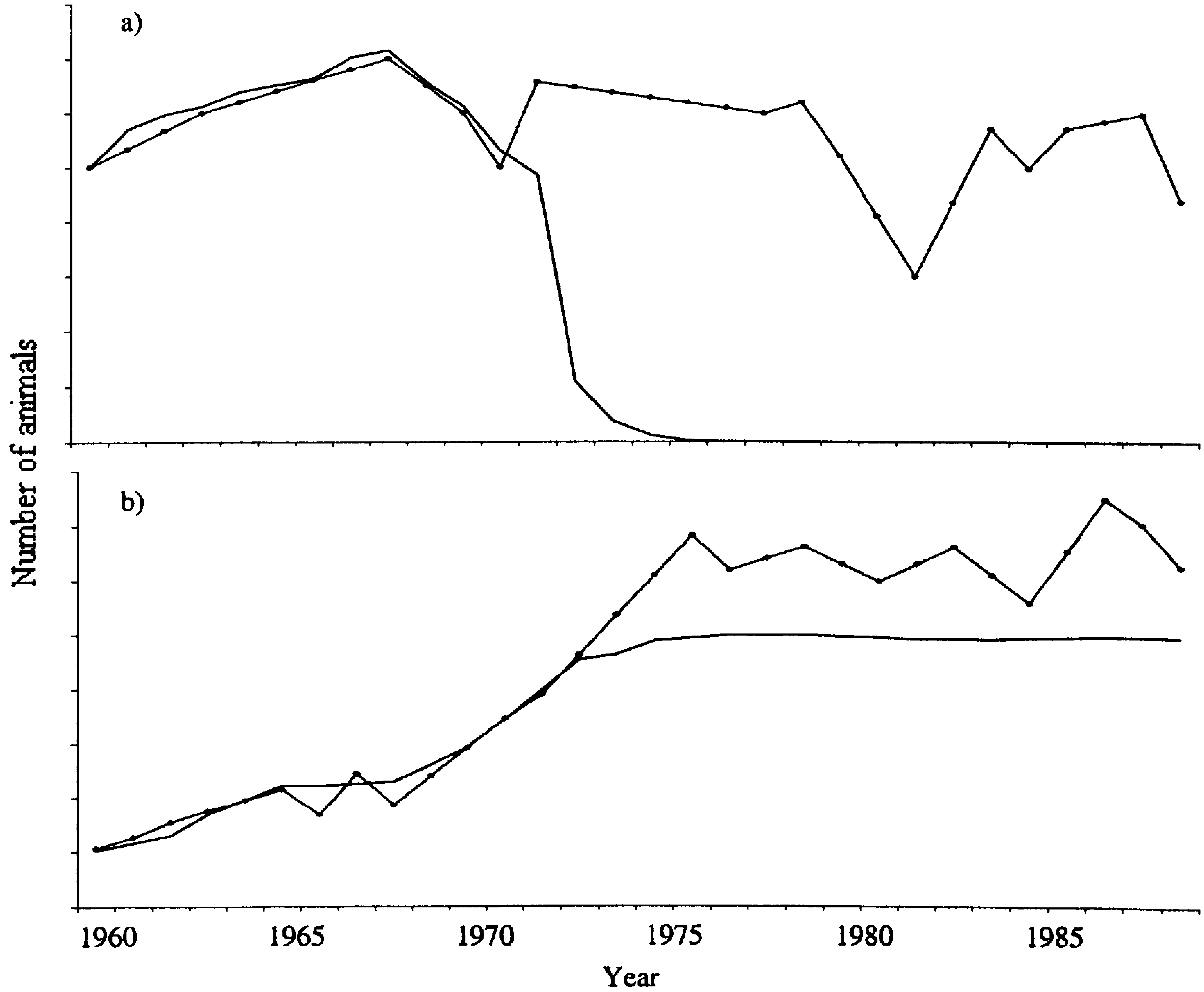

Figure 8.7 Annual populations numbers of a) migratory Thomson's gazelle and b) migratory wildebeest when component populations are restricted from increasing beyond natural population numbers. The solid line represents calculated numbers and the dotted line represents the estimated population numbers.

Interestingly, this appears to confirm that factors other than grass availability are constraining the population numbers of certain herbivores in the Serengeti. For instance, if grass production or the metabolic energy (ME) content of that grass were too high, then all herbivore components would be expected to reach natural population levels and even increase beyond them. Instead, these results indicate that either grass availability is underestimated and/or more specifically, the estimated ME content of green grass in zone 3 may be too low in the model (see section 5.3.2.1).

To test whether the latter is influencing population numbers, the ME content of green grass in zone 3 was increased at increments of 20 %, starting at a 10 % increase from the original value. Figure 8.8 illustrates that as the ME content of green grass increases, migratory Thomson's gazelle survival also increases. Furthermore, when ME content is increased by 90 %, calculated population numbers are equivalent to their estimated natural populations. However, with the highest recorded ME value of 14.06 MJ/kg for fresh new growth (which is a 54 % increase from the original value used in the model) it is unlikely that the average ME content of green grass will exceed this value or even be equal to it (Braun 1973; Duncan 1975; Sinclair 1975). Of course, as the original ME value used is an average based on Braun's data alone, it is possible that the energy content of grass could lie either above and below this value. Consequently, without further data to support an alternative to the ME figure used, it is impossible determine a value with any more accuracy. Nevertheless, even if the ME content of green grass nears a 54 % increase of the original value, this is not enough for migratory Thomson's gazelle to reach their natural population levels and subsequently is not the only factor that could be contributing to lowered population numbers.

As previously mentioned, a major factor contributing to the lack of primary productivity may be a lack of rainfall inputted into the model. One possible reason for this may be that the mean seasonal rainfall values used do not represent an average of the thirty years encompassed in the model (Sinclair 1977b, 1979b). Instead, they are likely to have been averaged from rainfall data over a shorter time-scale. Although Sinclair does not state this period, Norton-Griffiths *et al.* (1975) explain that their similar rainfall isohyets represent rainfall data taken from 62 rain gauges across the ecosystem during 1962 to 1972. These rainfall values are, therefore, only specific to those 10 years and likely to be an underestimate, as they do not include years during the mid-1970s when rainfall increased significantly (Sinclair 1979a; Hilborn & Mangel 1997; Mduma *et al.* 1999; Wolanski *et al.* 1999).

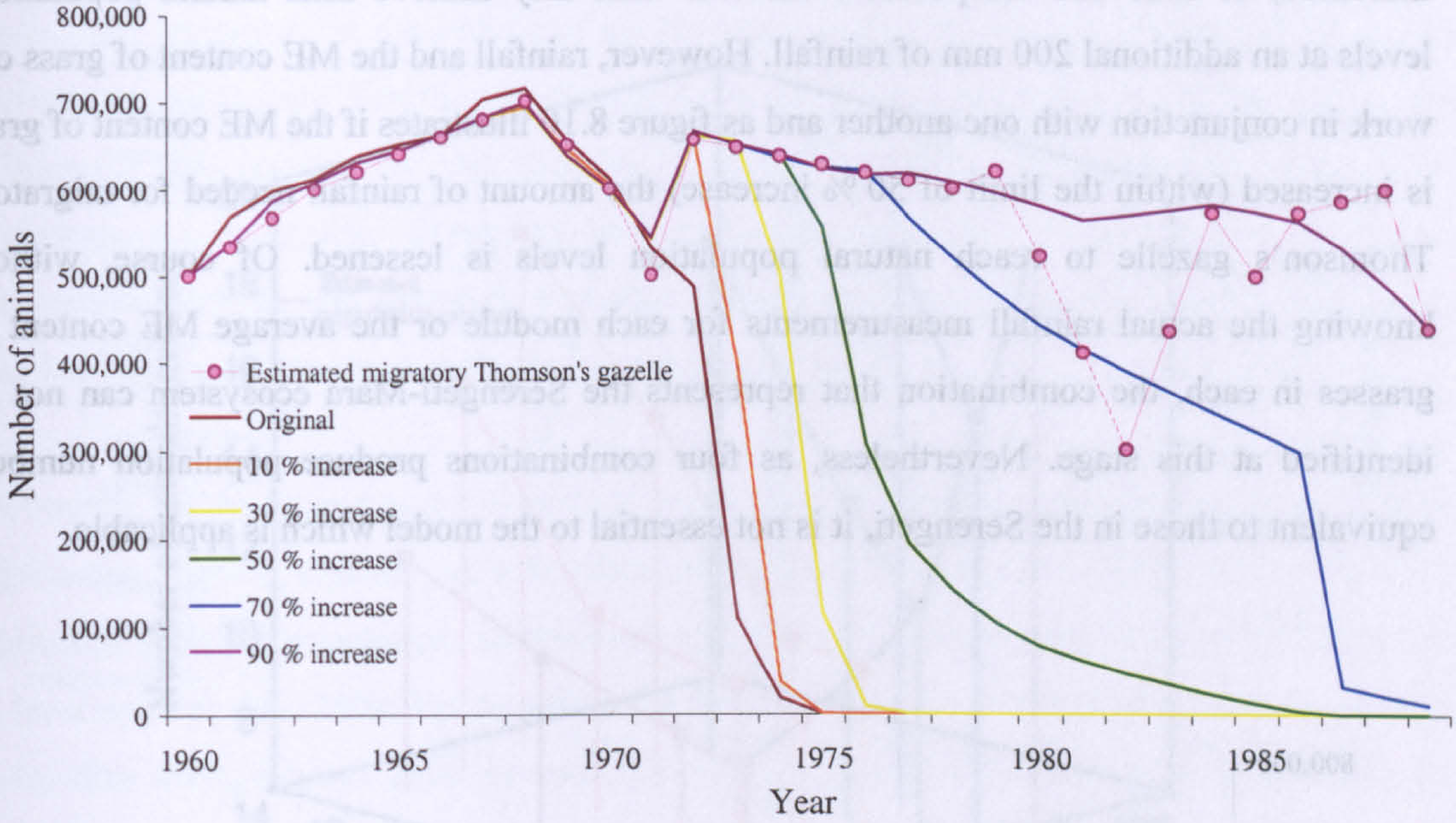

Figure 8.8 Annual populations numbers of migratory Thomson's gazelle when the metabolic energy content of green grass is increased.

In the light of this, a series of sensitivity tests were carried out to assess the effects of increased rainfall on herbivore components within the model. In order to proceed with this, it was initially considered that although Sinclair (1977b, 1979b) may have underestimated rainfall, his isohyets still adequately depicted seasonal and zonal variation required by the model. For instance, both Herlocker (1975) and Norton-Griffiths *et al.* (1975) support the latter variation in the rainfall gradient occurring across the Serengeti. In contrast, figure 3.2 illustrates that annual fluctuations in one season do not correspond to the other, nor does there appear to be any rationale behind the pattern (Herlocker 1975; Norton-Griffiths *et al.* 1975; Caro 1994; Wolanski *et al.* 1999). However, although the rainfall data given in figure 3.2 is taken from a single rainfall gauge on the Serengeti Plains, it does indicate that the average difference in rainfall between seasons over the 1960s, 1970s and 1980s were relatively similar (at 69 mm, 64 mm and 61 mm respectively; Caro 1994). This suggests that if Sinclair's rainfall data does indeed represent data collected between 1962 to 1972 (like those collected by Norton-Griffiths *et al.* 1975), then the difference in rainfall between seasons illustrated by his isohyets is likely to represent the overall average. The continued use of Sinclair's data was, therefore, assumed to be appropriate for the sensitivity test and subsequently this isohyet data was increased by increments of 50 mm. Using migratory Thomson's gazelle as an example, figure 8.9 shows that as rainfall is increased, so does this component's survival until they achieve their natural populations levels at an additional 200 mm of rainfall. However, rainfall and the ME content of grass can work in conjunction with one another and as figure 8.10 illustrates if the ME content of grass is increased (within the limit of 50 % increase) the amount of rainfall needed for migratory Thomson's gazelle to reach natural population levels is lessened. Of course, without knowing the actual rainfall measurements for each module or the average ME content of grasses in each, the combination that represents the Serengeti-Mara ecosystem can not be identified at this stage. Nevertheless, as four combinations produce population numbers equivalent to those in the Serengeti, it is not essential to the model which is applicable.

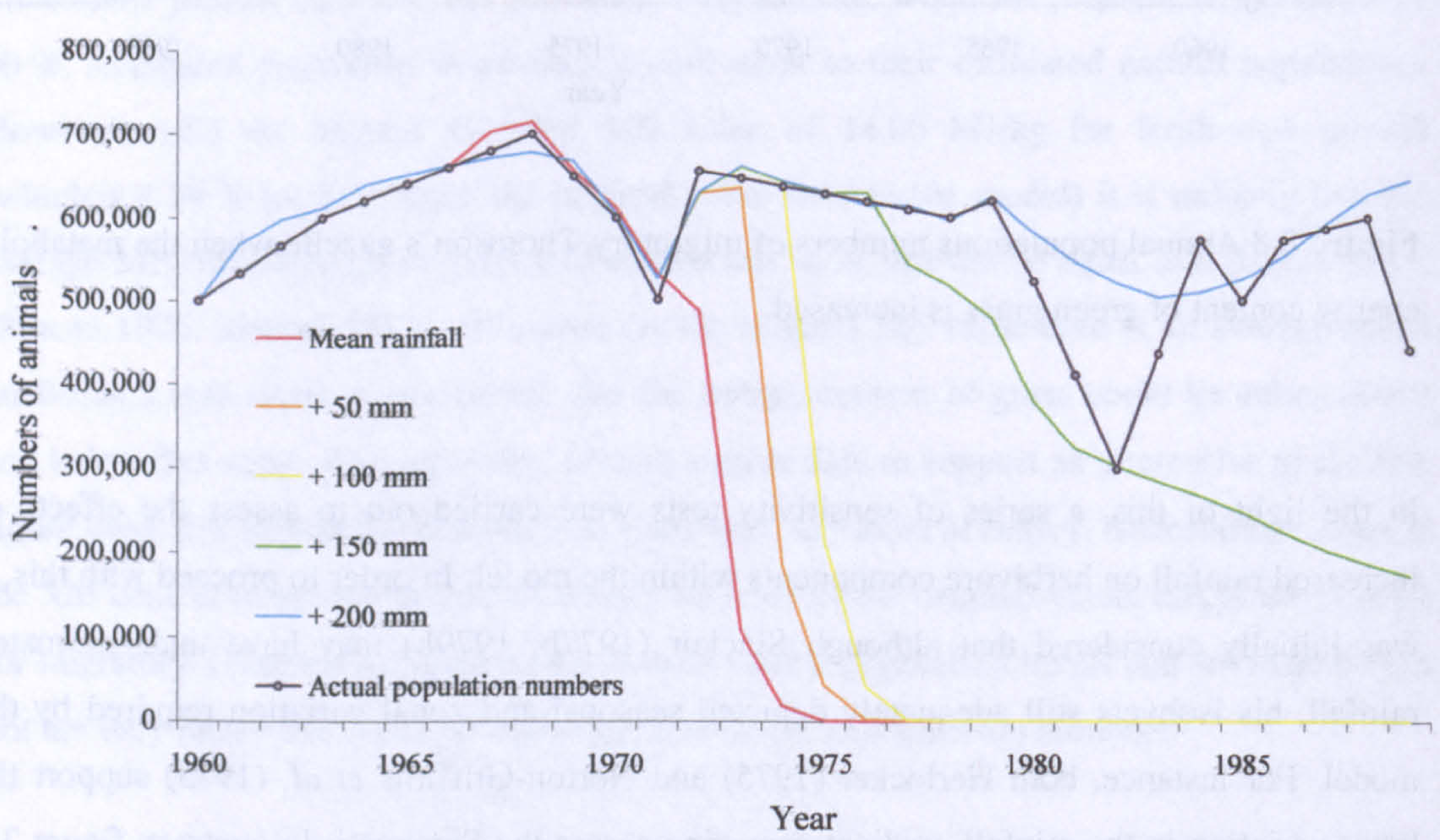

Figure 8.9 Annual populations numbers of migratory Thomson's gazelle when the mean rainfall figures are increased at increments of 50 mm (Sinclair 1977b, 1979b)

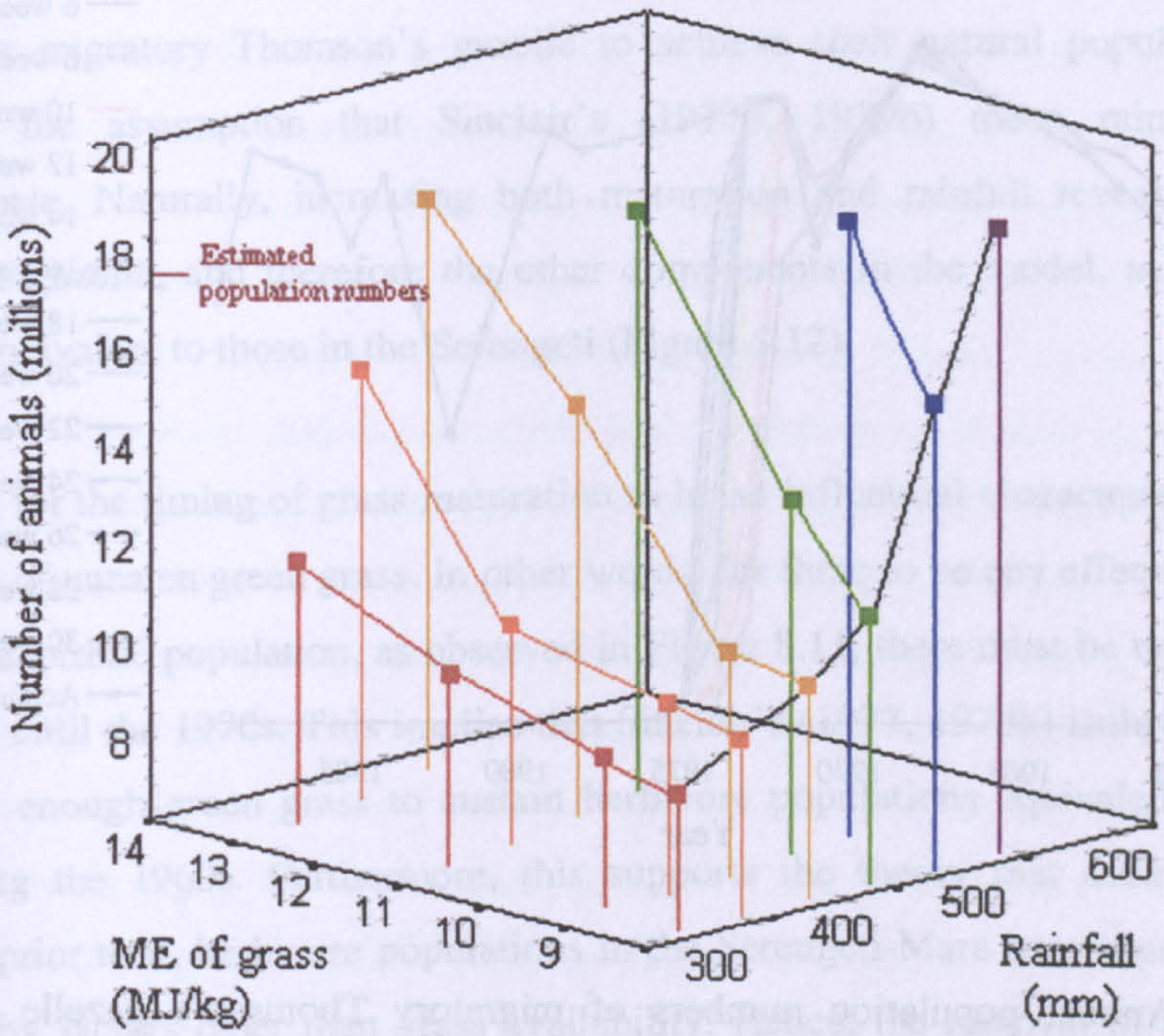

Figure 8.10 Annual populations numbers of migratory Thomson's gazelle when mean rainfall and the metabolic energy of grass is increased simultaneously. Each colour identifies a separate rainfall increment.

8.3.2 Maturation

As previously discussed in section 4.4.1, the point at which green grass matures to become dry grass (i.e. when crude protein content (*CP*) decreases below 4 %) is under debate. The information available on this subject is discordant and suggests that green grass can mature at any time from 5 weeks to 35 weeks, possibly more. However, the timing of maturation may have a significant influence on the dynamics of the model. That is, the longer it takes for grass to mature, the longer that grass will be available to herbivore components, and subsequently, more green grass will be available overall. A sensitivity test was, therefore, carried out to assess the impact of maturation on green grass availability, and consequently the population numbers of components in the model. As the current model already represents the outcome at 6 weeks, maturation was increased at two-week intervals from this starting point (Figure 8.11). Of course, for grass availability to increase by extending the maturation period, there has to be an excess of green grass for an equivalent number of weeks. To determine the likelihood of this occurring, a series of sensitivity tests were conducted in which rainfall was varied, and therefore, the amount of green grass available (Figure 8.12).

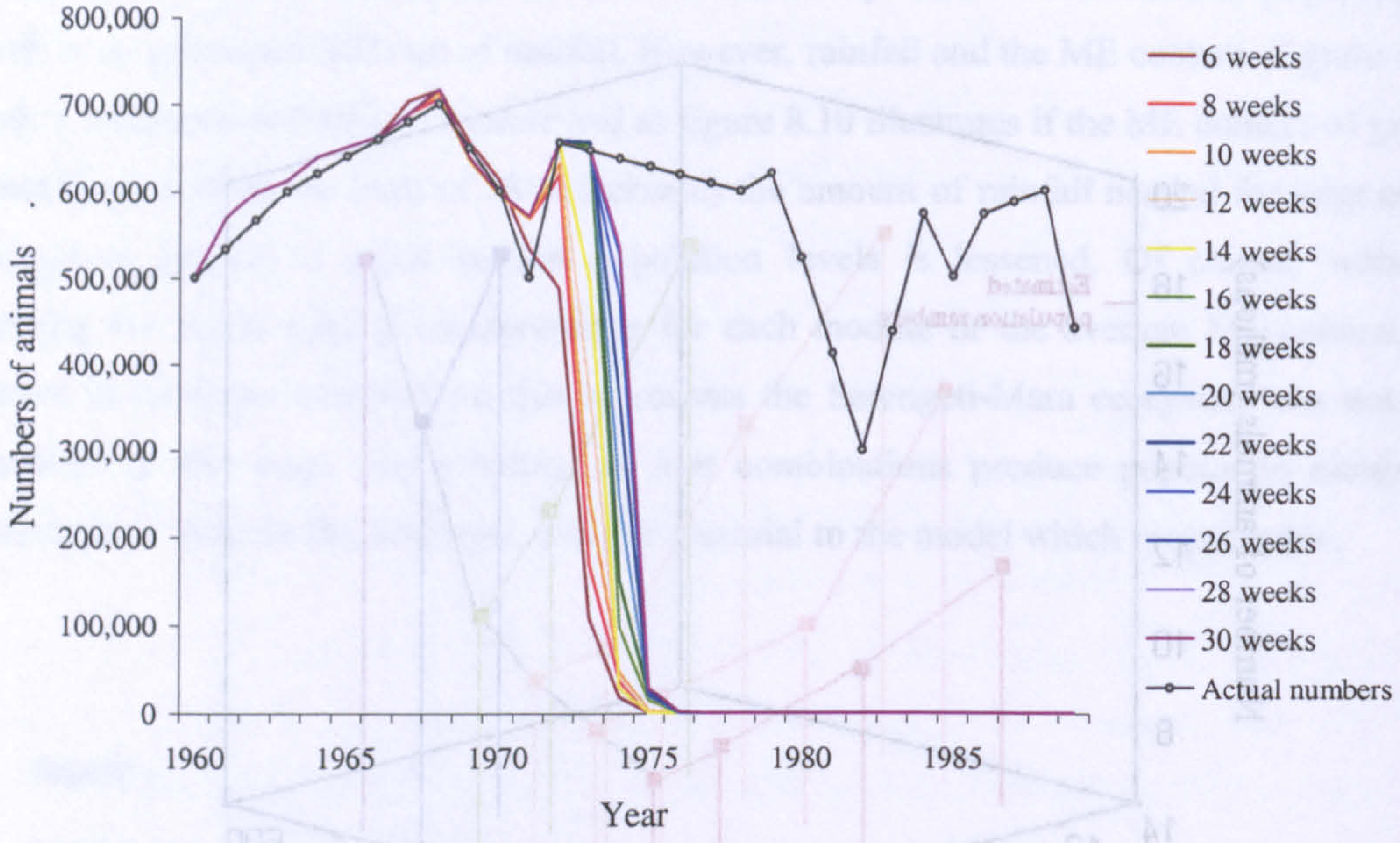

Figure 8.11 Annual population numbers of migratory Thomson's gazelle when mean seasonal rainfall values are applied (Sinclair 1977b, 1979b) and maturation is increased at 2 week intervals.

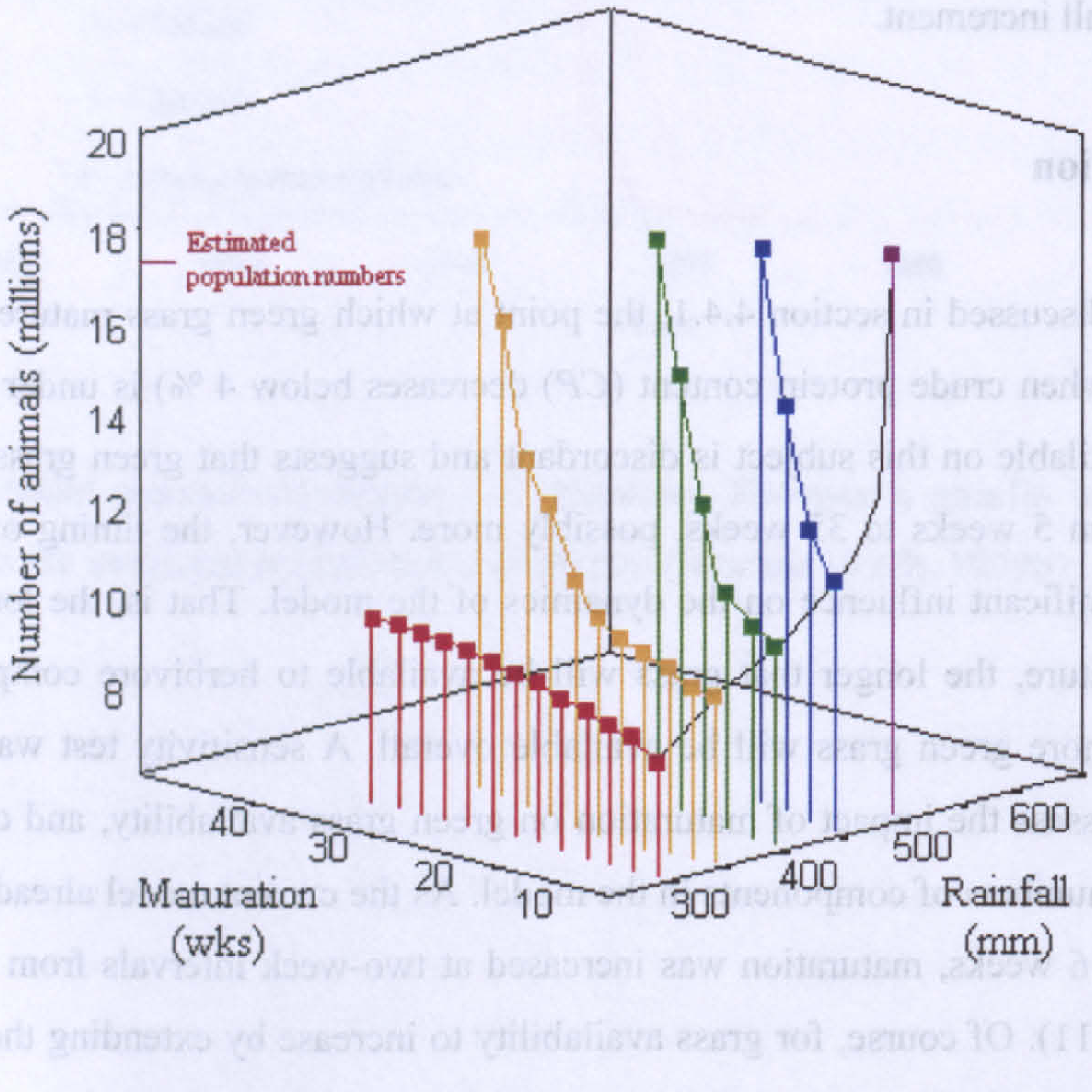

Figure 8.12 Annual population numbers of migratory Thomson's gazelle when seasonal rainfall values and maturation is increased. Each colour identifies a separate rainfall increment.

It is apparent from figure 8.11 that increasing the period at which green grass matures does have some influence on the herbivore components within the model. However, this is not enough for migratory Thomson's gazelle to achieve their natural population levels and reinforces the assumption that Sinclair's (1977b, 1979b) mean rainfall data is an underestimate. Naturally, increasing both maturation and rainfall reveals that migratory Thomson's gazelle, and therefore the other components in the model, achieve population numbers equivalent to those in the Serengeti (Figure 8.12).

Of course, for the timing of grass maturation to be an influential characteristic there must be a presence of uneaten green grass. In other words, for there to be any effect on the migratory Thomson's gazelle population, as observed in Figure 8.11, there must be unconsumed grass, at least up until the 1970s. This implies that Sinclair's (1977, 1979b) isohyet values provide more than enough green grass to sustain herbivore populations equivalent to those in the wild during the 1960s. Furthermore, this supports the theory that during this time and doubtless prior to it, herbivore populations in the Serengeti-Mara ecosystem were primarily regulated by factors other than grass availability. Hence, the removal of a limiting factor, such as rinderpest, resulted in both migratory wildebeest and buffalo populations increasing (see section 2.3.2; Sinclair 1973a, 1979d; Plowright 1982; Dobson 1995). The fact that they were able to increase confirms that there must have been excess grass available. As these two herbivore populations increased further, the amount of excess green grass decreased until grass availability could no longer sustain these herbivore populations and subsequently resulted in birth rates being equal to death rates, at which point wildebeest and buffalo numbers stabilised. This reasoning is certainly demonstrated by Mduma *et al.* 1999, who established that per capita food available to wildebeest was very high in the first half of the 1960s and decreased from here to became relatively constant in the 1980s.

Furthermore, if rainfall or maturation were greater than those combinations that fit natural population numbers, given in figure 8.12, then migratory wildebeest, at least, should have reached higher population numbers in the Serengeti. The fact that this has not happened suggests that either wildebeest are being restricted by factors other than grass availability, that rainfall and/or maturation do not exceed such levels or that other factors are influencing grass availability. Of course, if the actual rainfall data for each module were available, this indecision could be resolved to a certain extent. Therefore, although the model at present adequately depicts the dynamics of the Serengeti-Mara ecosystem, if the appropriate rainfall were included and the dynamics predicted in the model did not reflect those in the Serengeti, then other aspects that influence grass availability may need to be considered.

8.4 POSSIBLE FACTORS INFLUENCING GRASS AVAILABILITY

Undoubtedly, there are many factors that influence the amount of grass available to the grazing herbivores within each module. Of course, when constructing a model, it is only necessary to incorporate aspects that determine the overall dynamics of the ecosystem, thus, including every ecological factor is not only impractical, but also creates a model that is unnecessarily complex. To incorporate those factors that principally determine ecosystem dynamics, they first need to be identified and this is generally based on available information and personal judgement. The factor that is potentially the most influential is built into the model first and the resulting dynamics compared with those in the natural ecosystem. If these do not correlate, another potentially influencing factor can then be incorporated and so on. As previously mentioned, the model, at present, appears to represent the dynamics of the Serengeti-Mara ecosystem when a mortality constant prevents certain components from increasing beyond their natural levels and a specific amount of green grass is available. However, there is the possibility that rainfall estimates used in the model are not similar to those in the Serengeti, and if this is the case then other factors may be influencing the amount of grass available to grazing herbivores. Of the potential factors influencing grass availability, perhaps those requiring primary consideration are grazing, burning, nutrient cycling, the influence of other grazers and grass inaccessibility (de Vos 1969; Watson & Bell 1969; Braun 1973; Vesey-FitzGerald 1974; Pratt 1967; Lemon 1968; Lock 1972; Oliver & Laurie 1974; Sinclair 1975; Strugnell & Pigott 1978; McNaughton 1978, 1979a, b, 1985, 1992; Edroma 1981; Walker *et al.* 1981; Gillon 1983; Paige & Whitham 1987; Gichohi *et al.* 1996; McNaughton *et al.* 1997a, b; Hamilton *et al.* 1998; de Mazancourt *et al.* 1998; Drent & van der Wal 1999; Jefferies 1999).

8.4.1 Grazing

As previously mentioned in section 4.4, in order to estimate primary production more appropriately, other aspects of the dynamics of plant growth may need to be considered (Deshmukh & Baig 1983; Deshmukh 1984, 1986). Up until now, the only aspect of these dynamics incorporated in to the model has been the relationship between rainfall and grass growth under set conditions (see section 4.3; Braun 1973; Sinclair 1975). However, if these conditions are not equivalent to those occurring in the wild, then this may impugn the grass growth figures currently used. For instance, it is a well-established fact that compensatory plant growth may make-up for, and even over-compensate for, tissue reduction by herbivores (Jameson 1963; Vickery 1972; Jarmen 1974; Ryle & Powell 1975; Dyer & Bokhari 1976; Strugnell & Pigott 1978; McNaughton 1979a, 1992; Norton-Griffiths 1979; Edroma 1981;

Owen-Smith 1982). However, the extent to which grass availability increases is influenced primarily by the level of grazing a plant endures (Jameson 1963; McNaughton 1979a; Walker *et al.* 1981; Gichohi *et al.*1996). Under heavy grazing, the excessive reduction of above-ground productivity diminishes photosynthesis, which in turn suppresses any further growth (Jameson 1963; Milthorpe & Davidson 1965; Stoy 1965; Davidson & Milthorpe 1966; de Vos 1969; Gifford & Marshall 1973; Vesey-FitzGerald 1974; McNaughton 1979a, b). Between this extreme and the other, where grass is not grazed, there is an optimal level of grazing which promotes the maximum amount of regrowth (Crisp 1964; Noy-Meir 1975; Caughley 1976; McNaughton 1979a, b; Hilbert *et al.* 1981; Walker *et al.* 1981). McNaughton (1979a, 1985) has proposed a grazing model that illustrates this mechanism (Figure 8.13)

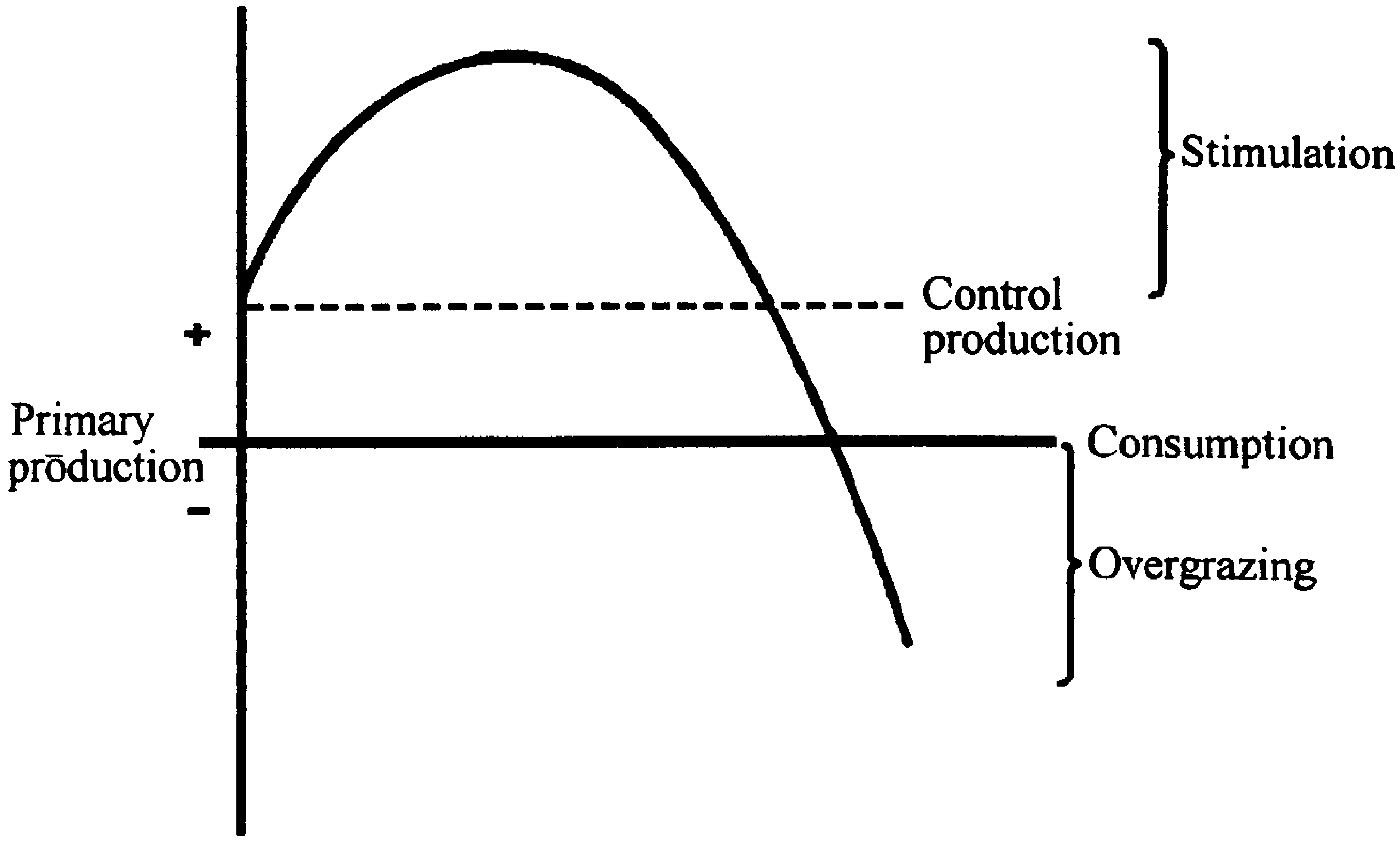

Figure 8.13 Hypothesis relating consumption by herbivores to net primary productivity of plants. The level of the control line (no grazing) is based on other factors regulating plant growth (McNaughton 1979a).

Figure 8.13, however, is only a general hypothesis, as the optimum level of regrowth varies depending on a large number of factors, including season, regularity at which grazing occurs, grass species, and subsequently, zone (Kinsinger & Shaulis 1961; Pratt 1967; Braun 1973; Gifford & Marshall 1973; Ryle & Powell 1975; McNaughton 1979a, b; Sinclair 1979a; Jefferies 1999). Consequently, the effects of grazing on each module needs to be addressed separately when considering grazing as a factor to be incorporated into the model. Furthermore, in order to estimate the influence of this factor annually, the relationships between grazing frequency and population numbers, and grazing intensity and population numbers, must first be defined. These require knowledge and data on the distribution, social organisation and grazing strategy employed by each component (Jarman & Jarman 1979; Jarman & Sinclair 1979; Pennycuick 1979; Seagle & McNaughton 1992).

8.4.2 Burning

The detrimental effect of fire on grass availability has already been incorporated into the model (see sections 4.4.2 & 4.5.1), but like grazing, the defoliation of grasses by burning can also stimulate compensatory growth (Ahlgren & Ahlgren 1960; Vesey-FitzGerald 1960; Kucera & Ehrenreich 1962; West 1965; Cushwa *et al.* 1968; Daubenmire 1968; de Vos 1969; Gillon 1983; Edroma 1984; McNaugton 1985; Moe *et al.* 1990). The amount of regrowth that occurs is primarily governed by the intensity and severity of the fire (Dix 1960; West 1965; Daubenmire 1968; Lock & Milburn 1971; Gillon 1983). West (1965) states that this depends to a large extent on the sum of combustible products either standing (dry grass) or accumulated in the form of litter. That is the more dry material that accumulates the more intense and damaging the fire (Vesey-Fitzgerald 1972; Eltringham 1976; Gillon 1983; Edroma 1984). Of course, the accumulated dry grass depends on prior grazing (Pratt 1967; Eltringham 1976). Heavy grazing reduces the amount of dry grass available as fuel, and subsequently, fires that do occur will be less severe. As the current model is set-up to predict the amount of dry grass that has accumulated each week, the severity of fires and therefore the effects of fire on regrowth could potentially be predicted. However, for this to be achieved the relationship between the amount of dry grass and fire severity and the relationship between fire severity and grass regrowth, must first be established.

8.4.3 Nutrient cycling

The recycling of nutrients from plant tissues to soils by herbivores is known to positively influence plant productivity and has been referred to as a 'quintessential feedback in grazing ecosystems' (Owen & Wiegert 1976, 1981; Stenseth 1978; Woodmansee 1978; Floate 1981; Dyer *et al.* 1986; Detling 1988; Huntley 1991; McNaughton *et al.* 1997a, b; de Mazancourt *et al.* 1998; Hamilton *et al.* 1998). The most obvious forms of recycling by herbivores is through faecal material and urine, as these supply the nutrients required by grass for compensatory growth (Lotera *et al.* 1966; Weeda 1967; McNaughton 1979b; Floate 1981; Jarmillo & Detling 1988; van Soest 1994; McNaughton & Banyikwa 1995; McNaughton *et al.* 1997a, b; de Mazancourt *et al.* 1998; Hamilton *et al.* 1998; Jefferies 1999). For example, a study by Hamilton *et al.* (1998) shows that increasing the N concentration, i.e. levels of urination, not only increases the amount of grass regrowth that occurs, but also reduces the detrimental effects of frequent grazing (Figure 8.14). However, it is not all mutualism between grasses and grazers, as an increased amount of faecal material can be detrimental to grass growth by obscuring leaves and subsequently reducing photosynthesis (de Vos 1969; Owen & Wiegert 1981; Jefferies 1999).

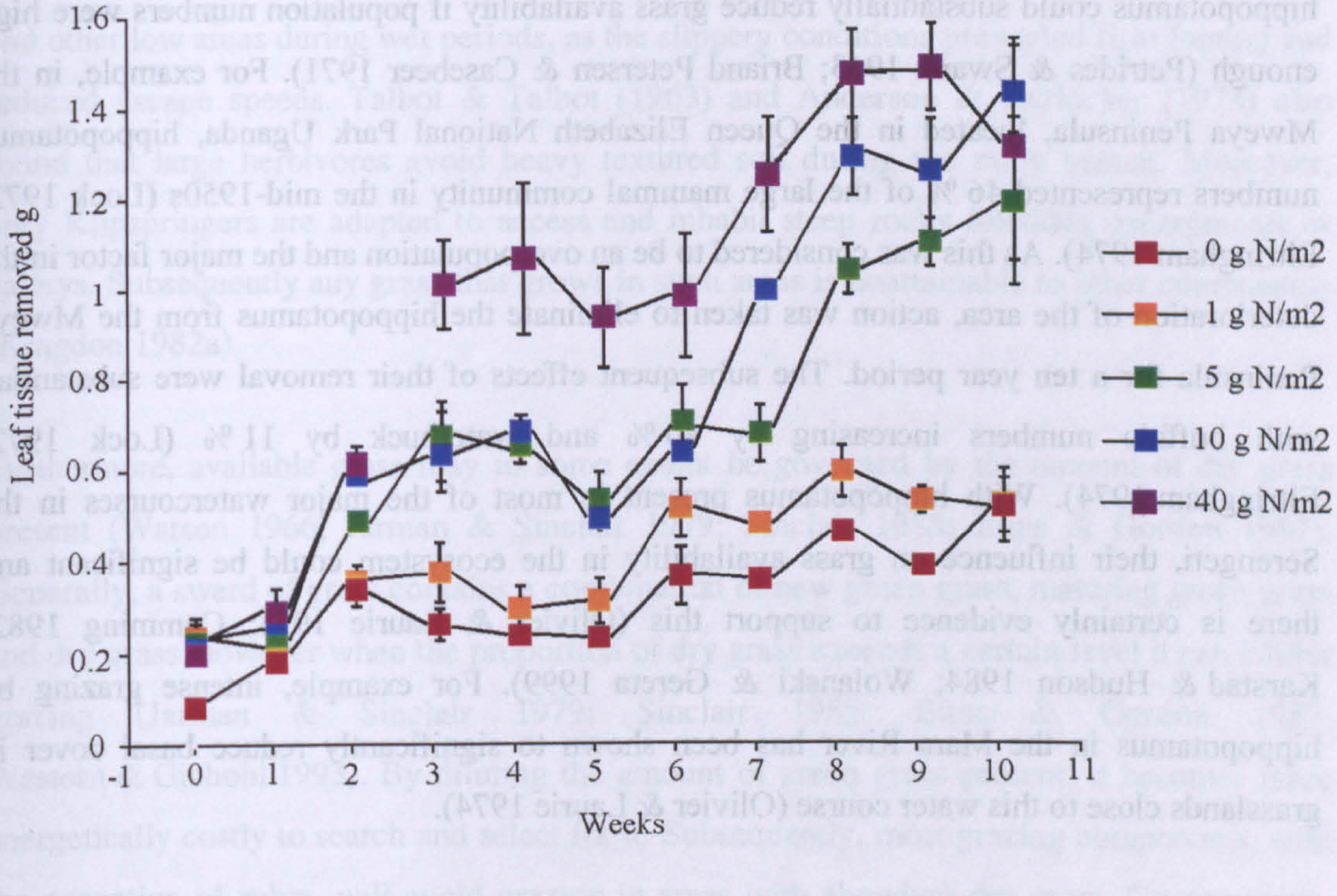

Figure 8.14 Weekly mean SE leaf tissue removed (g) in clipped plants at various nitrogen level applied throughout a 10-week experiment (Hamilton *et al.* 1998).

Another form of nutrient recycling by herbivores occurs through trampling (de Vos 1969; Walker *et al.* 1981). For instance, as grazers pass through an area, their movements not only cause dry material to enter the leaf litter layer, but also break-up this layer (de Vos 1969; de Mazancourt *et al.* 1998). However, increased numbers of herbivores can be detrimental by simply destroying the vegetation, and even moderate numbers of grazers can trample substantial amounts of green grass that would otherwise be available (Vesey-Fitzgerald 1960; de Vos 1969; Walker *et al.* 1981; Drent & van der Wal 1999).

In order to assess the extent to which these two forms of nutrient recycling influence grass growth and subsequently green grass availability in the model, further research is required on both subjects in relation to herbivore numbers.

8.4.4 Other grazers

Amongst the grazers and mixed feeders not included in the sub-unit modelled, two may potentially influence the overall dynamics of those components included. These are hippopotamus and the African elephant. The former is a non-selective grazer, and like the zebra, able to tolerate an exceptionally low-quality diet (Field 1969; Owen-Smith 1982; East 1984). Calculated to have a quantitative grass intake of 18 kg of dry matter a day, the hippopotamus could substantially reduce grass availability if population numbers were high enough (Petrides & Swank 1963; Briand Petersen & Casebeer 1971). For example, in the Mweya Peninsula, located in the Queen Elizabeth National Park Uganda, hippopotamus numbers represented 46 % of the large mammal community in the mid-1950s (Lock 1972; Eltringham 1974). As this was considered to be an overpopulation and the major factor in the deterioration of the area, action was taken to eliminate the hippopotamus from the Mweya Peninsula for a ten year period. The subsequent effects of their removal were substantial, with buffalo numbers increasing by 40 % and waterbuck by 11 % (Lock 1972; Eltringham 1974). With hippopotamus present in most of the major watercourses in the Serengeti, their influence on grass availability in the ecosystem could be significant and there is certainly evidence to support this (Olivier & Laurie 1974; Cumming 1982; Karstad & Hudson 1984; Wolanski & Gereta 1999). For example, intense grazing by hippopotamus in the Mara River has been shown to significantly reduce basal cover in grasslands close to this water course (Olivier & Laurie 1974).

The African elephant, in contrast, has been prominently recognised for its destructive utilisation of trees and their subsequent decrease (Croze 1974b; Eltringham 1980; Cumming 1982; Barnes 1983a, b; Pellew 1983; Ruess & Halter 1990; Ben-Shahar 1993; Spinage 1994; Leuthold 1996; van de Vijver *et al.* 1999). However, with a quantitative food intake of 22.5 kg DM/day, of which up to 88 % can constitute grass, the elephant may also significantly influence the amount of grass available to other grazing components (Buss 1961; Petrides & Swank 1963; Watson & Bell 1969; Laws 1970; Ruggiero 1992; Spinage 1994). Consequently, the inclusion of the elephant and/or the hippopotamus in the model may be necessary if the dynamics it predicts do not follow those in the wild.

8.4.5 Inaccessible grass

Another factor likely to have a significant influence on grass availability and potentially limit population numbers of grazing components is the accessibility of grass (Lamprey 1963; Sinclair 1983, 1985). The presence of bushes and trees in Zone 1 and 2, can make some grass difficult to graze, particularly for larger grazing species. Consequently, the total amount of grass available may be substantially lower than predicted by the model. A similar situation may occur between topographically varying areas within the Serengeti (Lamprey 1963; Jarman & Sinclair 1979; Stelfox & Hudson 1986). For example, Stelfox & Hudson (1986) state that both gazelle species generally avoided valley bottoms and other low areas during wet periods, as the slippery conditions prevented firm footing and reduced escape speeds. Talbot & Talbot (1963) and Anderson & Herlocker (1973) also found that large herbivores avoid heavy textured soil during the rainy season. Moreover, only Klipspringers are adapted to access and inhabit steep rocky hillsides, escarpments or valleys. Subsequently any grass that grows in such areas is unattainable to other components (Kingdon 1982a).

Furthermore, available grass may to some extent be governed by the amount of dry grass present (Watson 1966; Jarman & Sinclair 1979; Sinclair 1985; Illius & Gordon 1987). Generally, a sward of grass contains a combination of new green grass, maturing green grass and dry grass, however when the proportion of dry grass exceeds a certain level it can inhibit grazing (Jarman & Sinclair 1979; Sinclair 1985; Illius & Gordon 1987; Western & Gichohi 1993). By diluting the amount of green grass present, it becomes more energetically costly to search and select for it. Subsequently, most grazing components, with the exception of zebra, will avoid grazing in areas with abundant dry grass. Consequently, the amount of grass that is accessible to grazing herbivores may reflect on the dynamics of those herbivores within an ecosystem.

8.5 POSSIBLE FACTORS LIMITING POPULATION NUMBERS

As previously mentioned in section 8.3.1, the population numbers predicted by the model indicate that factors other than grass availability may be primarily regulating certain component populations. Although such regulating factors are beyond the scope of the current model, by identifying those potentially responsible for the population dynamics of each component, their overall importance to the ecosystem may be assessed in the future. Those factors that may be potentially influential and therefore require future consideration are the social organisation of each component, their selectivity and any additional sources of mortality (Jarman & Jarman 1973; Senzota 1988).

8.5.1 Social organisation

The organisation and social behaviour of a herbivore population are considered to be integral factors in the acquisition of grass by that herbivore (Geist 1974; Jarman 1974; Jarman & Jarman 1973, 1979; Underwood 1981, 1983; Sinclair 1983). The extent to which a herbivore is constrained may be determined by the degree of social organisation within that herbivore's population (Jarman & Jarman 1973, 1979). For instance, extreme territorial behaviour has been found to act as a population regulating mechanism, modifying or overriding resource availability (Jarman & Jarman 1973; Geist 1974). This is because individuals within each territory are dependent on their patch supplying an adequate amount of grass. Consequently, variations in patch quality and the occurrence of localised rainfall, causes considerable competition between individuals, or groups of individuals, for the better patches (Duncan 1975; Jarman & Jarman 1979; Thouless & Guinness 1986; Clutton-Brock *et al.* 1986, 1987b). For example, impala are known to be territorial and although their territoriality is not considered extreme, it has been shown to effect their overall reproductive potential (Jarman & Jarman 1973). In contrast, migratory wildebeest have very little social organisation. As a result, individuals are free to distribute themselves according to the availability of resources (Jarman & Jarman 1973, 1979). However, of all the species incorporated in to the model, zebra appear to have the most restrictive social organisation, in the form of fixed membership herds (Jarman & Jarman 1979; Saltz 2002). This may potentially be causing population numbers in the Serengeti to be much lower, than those predicted in both the current model and a study carried out by Senzota (1988) to investigate zebra population dynamics in the Serengeti.

8.5.2 Selectivity

Currently, the degree of food selectivity by components incorporated into the model is relatively basic. With the exception of zebra (<4 % *CP*), most of the components are limited to eating green grass (with a maximum of 24 % crude protein content and a minimum of 4 % *CP*). However, if any of the grazing herbivores included in the model are more selective in terms of crude protein content, then the amount of grass available to them predicted by the current model will be an overestimate (Watson 1966; Jarman & Sinclair 1979; McNaughton 1985). Such specific foraging preferences are well known amongst ungulates, and a number of studies have shown that this is manifested in the active search and selection of new growth, particular plant parts and specific grass species, all with higher *CP* contents (see section 4.4.1; Gwynne & Bell 1968; Stewart & Stewart 1970; Sinclair & Gwynne 1972; Jarman 1974; Duncan 1975; Field 1975; Kreulen 1975; Jarman & Jarman 1979; Jarman & Sinclair 1979; Spinage *et al.* 1980; Kingdon 1982b; Owen-Smith 1982; Sinclair 1983, 1985; Hansen *et al.*1985; McNaughton & Georgiadis 1986; Estes 1991). These investigations also reveal an allometric relationship between selectively and body weight. For example, buffalo, considered to be bulk feeders, show relatively no selectively in comparison to Thomson's gazelles, who rarely consume anything other than fresh green grass, grass leaves and short grass species (Sinclair 1977b; 1983, 1983; Kingdon 1982a, b; Underwood 1983; Beekman & Prins 1989). Of course, Thomson's gazelle are at an advantage when such grass is readily available, as they can exceed energetic requirements with little effort (Jarman & Sinclair 1979). However, when this good quality forage becomes difficult to obtain, they are forced to spend more time searching and subsequently, energetic requirements are not met so readily (Beekman & Prins 1989).

Furthermore, a herbivore's morphology and physiology can also prevent it from consuming otherwise available grass (Sinclair 1985; Illius & Gordon 1987, 1991; Wilmshurst *et al.* 1999a). For instance, on short grass swards the quantity of grass cropped in each bite is smaller than that in long grass swards (Black & Kenney 1984; Laca *et al.* 1992; Gross *et al.* 1993a; Wilmshurst *et al.* 1999a). While smaller herbivores are constrained from grazing on taller swards, as the quantity of grass in a single bite exceeds their mouth dimensions, larger herbivores are constrained by the grazing rate (mass of grass cropped per unit time) when feeding on shorter grass swards (Lamprey 1963; Allden & Whittaker 1970; Sinclair 1974d; Hodgson 1985; Stelfox & Hudson 1986; Illius & Gordon 1987; Spalinger & Hobbs 1992; Owen-Smith & Cumming 1993; Wilmshurst *et al.* 1999a). The abundance of different sward heights may, therefore, be limiting the amount of grass available to particular grazing components in the Serengeti.

8.5.3 Other mortality

Three forms of mortality, in addition to that caused by food shortages, have been recognised to be influential in the population dynamics of grazing herbivores in the Serengeti. These are predation, disease and poaching. Although the former is included in the model it represents an average minimum, that is the lowest predation rate required by the five major carnivores to just sustain their population numbers (see section 7.2). It does not take into account that these carnivores could potentially consume more, that females have to eat more to reproduce successfully, or that those carnivores (such as jackals) not included in the model may add to the predation quota of some components.

However, even in the current model it is evident that hartebeest are strongly influenced by predation. Figure 8.15 illustrates the effect of increasing predation at 10 % increments, as well as removing it altogether, on hartebeest population numbers. Although a 10% increment may appear excessive, as the predation of hartebeest is so low, this only represents a small number of individuals (7 juveniles and 6 adults predated in the dry season and 8 young, 4 juveniles and 6 adults in the wet season). This indicates that as hartebeest population numbers are relatively low, they are very sensitive to the loss of individuals. Predation may, therefore, have a strong influence on hartebeest dynamics.

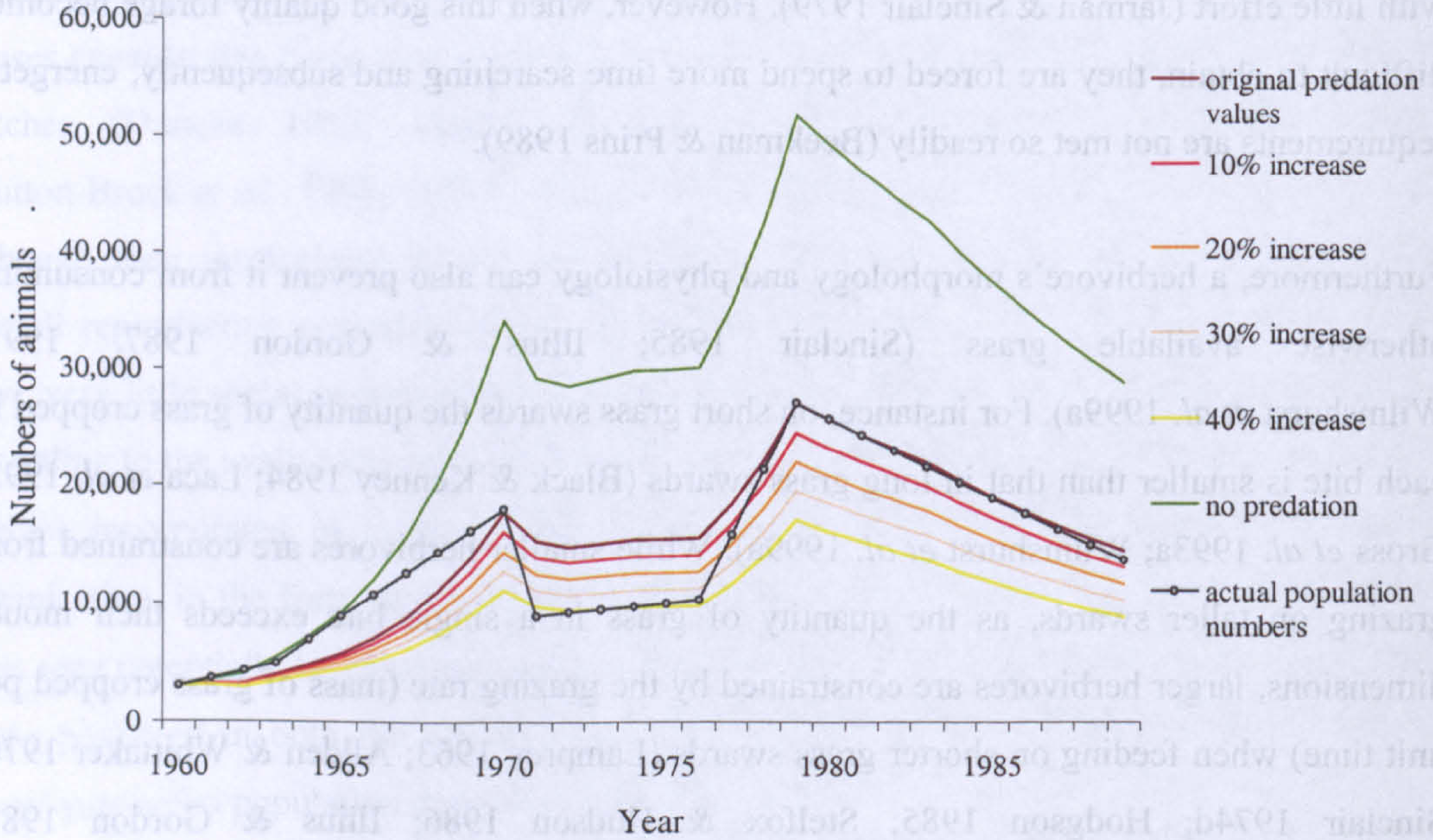

Figure 8.15 The effect of increasing predation by 10 % increments and removing it from hartebeest populations in the model.

Poaching is considered by many to threaten the population viability of certain herbivores within the Serengeti-Mara ecosystem (Talbot & Talbot 1963; Dublin *et al.* 1990; Arcese *et al.* 1995; Campbell & Borner 1995; Sinclair 1995a; Baldus *et al.* 1997; Krebs *et al* 1999). As discussed in section 1.3, closure of the Kenyan border led to a decrease in anti-poaching patrols in the Serengeti during the early to mid-1980s. One of the primary consequences of this was the substantial decrease in buffalo numbers through increased illegal hunting, as shown in figure 8.2 (Dublin *et al.* 1990; Campbell & Borner 1995; Baldus *et al.* 1997; Krebs *et al* 1999). Therefore, as poaching and trophy hunting have always contributed to the off-take of many of herbivores in the Serengeti, primarily towards the western boundaries where human settlement is greatest, it is likely that their populations may be affected by this mortality factor (Talbot & Talbot 1963; Hofer *et al.* 1993; Campbell & Hofer 1995; Caro *et al.* 1998; Mduma *et al.* 1998; Krebs *et al* 1999).

The occurrence of disease induced mortality, independent of grass shortages, as discussed in section 5.5.3, has not been recorded in the Serengeti-Mara ecosystem since the removal of rinderpest (Plowright 1982; Prins & Weyerhaeuser 1987; Campbell & Borner 1995; Dobson 1995). It was, therefore, assumed that the population dynamics of herbivores in the Serengeti have not been regulated or influenced by disease during the time-scale of the model. However, this may not be a correct supposition, as Saltz (2002) states that zebra are sensitive to regular epizootics as a consequence of their social structure. He found that as females remained in close contact with each other within groups, this maximised the probability of epizootic transmission. Moreover, the high rate of individual movement between groups then promotes the rapid transmission of such diseases. As outbreaks most likely occur at low, but sustained levels, this may to some extent explain why disease related mortality has gone unidentified. Consequently, the influence of such diseases on the population dynamics of herbivores within the Serengeti may be potentially significant.

8.6 CONCLUSIONS

As it stands, the current model, its set-up, the aspects of the Serengeti-Mara ecosystem that have been incorporated and the data that has been included, have revealed that not all grazing herbivore populations are being regulated primarily by their food resource. Of those that are, only migratory wildebeest appear to be regulated by grass availability throughout the time-scale applied to the model. In comparison, migratory Thomson's gazelle and Grant's gazelle remain uninfluenced by grass availability until wildebeest numbers increased two-fold from their 1960 starting figure. Furthermore, if migratory wildebeest are allowed to increase above their natural populations in the model, both Grant's gazelle and migratory

Thomson's gazelle numbers decrease, and if either Grant's gazelle or migratory Thomson's gazelle are forced to increase, wildebeest numbers then decrease. This suggests that there is a strong competitive link in the model between these three components specifically during the wet season in zone 3. The question is 'are the predictions made by the model incorrect, and therefore, need to be reassessed, or is there evidence, not only to support the existence of this competitive interaction within the Serengeti, but also its strength.

The general consensus is that migratory wildebeest populations are only limited by dry season grass production in the zone 1 (Sinclair 1974d, 1975; Sinclair *et al.* 1985; Stelfox & Hudson 1986; Fryxell *et al.* 1988; Murray *et al.* 1992; Pascual & Hilborn 1995; Hilborn & Mangel 1997; Pascual *et al.* 1997; Krebs *et al.* 1999; Mduma *et al.* 1999). However, this view appears to be based on only one study carried out by Sinclair (1977b; 1979c) from 1960 to 1977. From this, Sinclair stated that following record high dry season rainfall in 1971 (which according to Hilborn & Mangel (1997) was 25 mm more than the highest recorded rainfall in the 1960s; Table 4.1), migratory wildebeest and buffalo numbers began to increase steeply. On this evidence, Sinclair proposed that migratory wildebeest and buffalo were regulated by dry season grass production. However, according to census data, migratory wildebeest began their steep increase in 1968, while such an increase is not even evident in the buffalo population, even though the census data was primarily collected by Sinclair (1973b, 1974d, 1977a, 1979c; Figures 8.1 & 8.2). As a result of Sinclair's proposal, when wildebeest populations appeared to stabilise in 1978, it was automatically assumed that this was due to dry season rainfall returning to its supposed norm, therefore reducing the amount of grass available to migratory wildebeest and thus limiting their numbers. However, it was never questioned why buffalo continued to increase until 1980 following two years of lowered dry season rainfall (Table 4.1). Furthermore, there is no evidence to suggest that the increase in migratory wildebeest numbers influenced any of the other herbivore populations in zone 1 through the competition for grass, which at least to a certain degree would be expected (Sinclair 1974d).

On the other hand, a study by Borner *et al.* (1987) demonstrates that the migratory Thomson's gazelle populations have decreased following the increase in wildebeest numbers (Figure 8.16). In their study, they conclude that predation, interspecific competition and disease could have contributed to this decline. However, the latter is based on parasite burdens increasing during the decline and as previously discussed most animals become more susceptible to parasitic diseases, as well as predation, when they are in poor condition (see section 5.5.3). The increase in predation and parasites on Thomson's gazelles, therefore, merely implies that food resources were inadequate at the time. Of course, some predator populations have increased steadily since the 1960s (see section 7.2.4) and this could have caused the decline in gazelle numbers. However, in the current model, although only basic predation rates could be employed, this increase in carnivore numbers has been included and had not been particularly influential on population numbers.

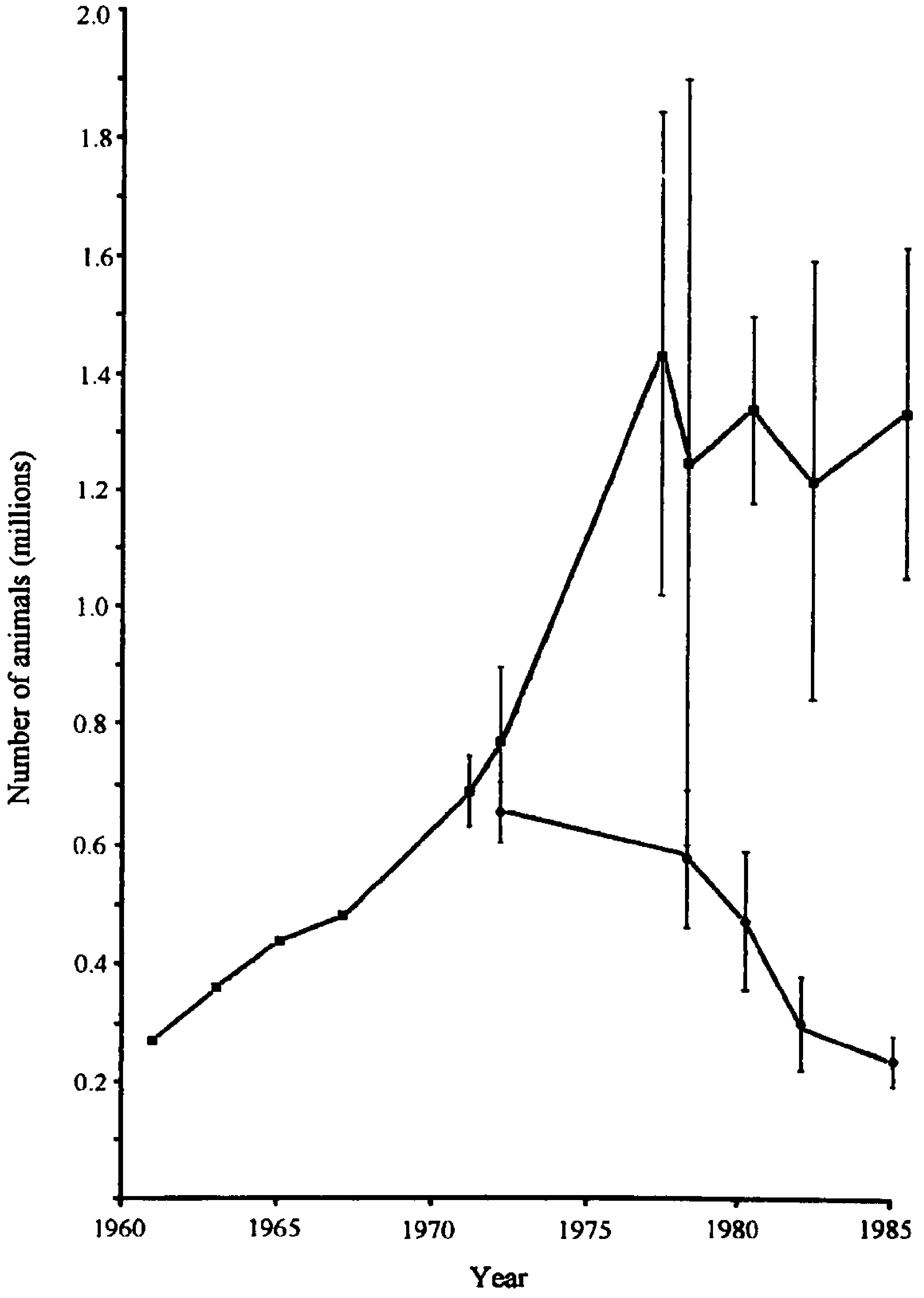

Figure 8.16 Changes in the Serengeti, migratory Thomson's gazelle population (circles indicate mean and 95% confidence limits are plotted against time) and wildebeest population (squares; Borner *et al.* 1987).

Furthermore, if predation is increased at increments of 10 %, as applied to hartebeest in figure 8.15, migratory Thomson's gazelle population only begin to show a similar decline to that in figure 8.16 when predation is increased by 50 % (an addition of approximately 16,000 individuals predated annually during the 1980s). The occurrence of this level of predation is debatable considering that both cheetah and African wild dog, which primarily prey on Thomson's gazelle (see section 7.2.2), have decreased substantially in numbers from the 1960s. In other words, for lions and hyaenas to have increased their preference for Thomson's gazelle in the 1980s, despite migratory wildebeest becoming very abundant, is unlikely. In light of this, the only remaining feasible explanation for the decrease in migratory Thomson's gazelle recorded by Borner *et al.* (1987) and Sinclair & Norton-Griffiths (1982) is interspecific competition either in zone 2 during the dry season, zone 3 during the wet season or both. As no other herbivore populations, apart from migratory wildebeest (as illustrated in figure 8.15), show a corresponding change in numbers to that of migratory Thomson's gazelle, this suggests that the increasing numbers of wildebeest intensified the competition for grass between these two species (that is in zone 3 during the wet season). A situation that has not only been recognised by Sinclair (1995b), but also led to him proposing that overgrazing could be occurring on the plains, i.e. zone 3.

Moreover, Sinclair & Norton-Griffiths (1982) predict that when competition for a common (food) resource is asserted, at least one population should level off or go down as another continues to go up or levels off. Hence, Thomson's gazelle are seen to decrease at the same time as wildebeest appear to stabilise in the Serengeti (Borner *et al.* 1987). This same pattern is also evident in the model. Consequently, when grass availability is limited in the model, wildebeest stabilise while Thomson's gazelle gradually decrease. This indicates that the methods used to set-up the model, such as the application of metabolic rates to predict survival, were successful in replicating the dynamics of the Serengeti-Mara ecosystem. The implications of which are discussed in chapter 9.

CHAPTER 9: DISCUSSION

9.1 THE MODEL THUS FAR

The aim of this research was to initiate the construction of a comprehensive model delineating the dynamics of the Serengeti-Mara ecosystem. The creation of a user-friendly design was hoped, not only to achieve a greater understanding of this ecosystem, but also to eventually guide management and conservation decisions in the future. This study has focused on the processes involved in setting-up such a model, beginning with its basic foundation of accommodating the spatial and temporal variation in climate and physiography across the Serengeti region (Chapter 3). This is followed by an investigation of the relationship between grass growth and rainfall, along with the mechanisms concerned with limiting grass availability (Chapter 4), the subsequent survival and recruitment of grazing herbivores (Chapters 5 & 6) and finally, the influence of predation upon these herbivores (Chapter 7). The effectiveness of the model at depicting this sub-unit of the Serengeti-Mara ecosystem was investigated and a number of hypotheses were drawn from the results (Chapter 8). This final chapter discusses the successes and shortcomings of the methods and data used in the set-up of the model, the implications of the results, the scope and direction of future work, and the inference of all of these for the conservation of the Serengeti-Mara and potentially other savannah ecosystems.

9.2 The pros and cons of the model

It is the substantial amount of research data available on the Serengeti-Mara ecosystem that has provided a strong basis on which to construct a simulation with the potential to encompass many elements of the ecosystem. However, even with this abundance of data, during the development of the model it was occasionally found that either the data available was discordant, and subsequently difficult to determine the most appropriate values to use, or the data was simply inadequate. Wherever possible in these situations, a less conventional method, for which sufficient data was available, was applied to model. For example, as very little usable data has been collected on the annual survival rates of the different herbivore populations in the Serengeti, the relative metabolic rates of each herbivore species were acquired instead (see section 5.3). These were used to create survival curves based on the daily amount of food required to sustain different sized individuals in each population. This method proved more than adequate for the model, as metabolism in animals is a heavily studied subject with relatively substantial amounts of reliable data. Consequently, metabolic rates were not only used to estimate the minimum intake required by each herbivore, but also to calculate predation rates of carnivores (section 7.2.1), as well as the additional intake required by females to conceive, gestate and support their young, thus incorporating the effects of grass availability on recruitment (section 5.4). The fairly uniform application of this method throughout the model also maintained consistency and minimised programming errors.

Although, the use of RMRs was an effective alternative in estimating the amount of food required by different individuals, the separation of individuals into various groups based on their foraging efficiency proved to be unsuccessful (section 5.3.2.2). This was due to very limited empirical data on the behavioural aspects of foraging variation. Subsequently, methods could only be based on very tenuous assumptions and this produced results that could not be compared or confirmed. As a result the inclusion of foraging variation in the model was abandoned and the variation in RMR between different sized individuals was the only form of variation to be incorporated. As it happens, the addition of further individual variation within each herbivore population, did not appear critically influential in the overall dynamics of the model and may have added to the models complexity unnecessarily. Nevertheless, this has highlighted that foraging efficiency amongst individuals is a relatively untouched area of research that doubtless requires some attention.

In other parts of the model, where more essential data was inconsistent or insufficient, sensitively tests where applied to investigate whether the input of potentially inaccurate data would have significant effects on the overall dynamics of the ecosystem. For instance, there were initial concerns about the weight range data for each African mammal species differing, in some instances quite substantially, between sources (section 5.3.2.1). Whether these varying ranges are a result of differences in sampling methodologies cannot be confirmed, but it is one explanation. This demonstrates that determining the most appropriate data from that available can be a dubious, if not an impossible exercise. In other words, it may not be feasible to choose between, or even compare, sets of empirical data acquired through the application of different methodologies on the same topic, if they vary significantly. In the case of the weight range dispute, a sensitively test revealed that relatively inaccurate weight data, when applied to the model, would have little influence on the survival rate of each species and was thus no longer a primary concern (section 5.3.4). However, the discordancy between sources that identified the decline in crude protein content of grass over time, was insurmountable (sections 4.4.1 & 8.3.2). A sensitivity test, not surprisingly, revealed that the longer it took for grass to decline in its crude protein content, the longer that grass was available for consumption by grazing herbivores. More unexpected, was that this profoundly influenced the dynamics of the ecosystem in the model by providing an abundance of additional consumable grass as the period of crude protein decline was extended. This, though, depended on two factors, the amount of grass growth, primarily due to rainfall, and the number of grazing herbivores present. Unfortunately, as there was also controversy and subsequently uncertainty surrounding the available rainfall data, this further complicated the situation by increasing the number of possible outcomes (section 8.3.1). Moreover, out of the combinations of rainfall and grass maturation run in the model, a number of them produced herbivore populations that behaved similarly to those in the Serengeti. It was, therefore, impossible, without further field-work on grass maturation and appropriate rainfall data, to determine which combination was equivalent to that in the wild. Nevertheless, the combination used in the model is inconsequential to its overall dynamics, as the outcome of each simply reflect the same amount of available grass for herbivore consumption.

The final crux of the model was whether the dynamics of the ecosystem predicted by the model, not only appeared similar to that of the Serengeti, but also behaved the same. One way of testing this is to compare the responses of individual herbivore species predicted in the model with those evident in the wild. For example, in the model, as the amount of grass present is reduced, there is an order by which different grazing herbivore populations respond to such a limitation. This is primarily due to the application of the metabolic rates used to estimate survival. Consequently, the smallest herbivore species, in this case the Thomson's gazelle (requiring proportionally more food to survive) is the first to be influenced by reduced grass availability, while the largest animals, such as the buffalo, are the last to respond. In the Serengeti, there is evidence to support this sequence of response. In a study by Borner *et al.* (1987) it was revealed that at the same time as the migratory wildebeest population appeared to stabilise following a substantial increase in their numbers, migratory Thomson's gazelle numbers decreased gradually. Therefore, as food became limited by the abundance of herbivores, although wildebeest were affected, Thomson's gazelle were affected more and this indicates a relationship between response to food limitation and size. Furthermore, the degree of response by these two natural populations is also equivalent to that predicted in the model. One of the primary factors contributing to this degree of response is the inclusion of food-limited recruitment. Consequently, low levels of recruitment led to wildebeest numbers stabilising and restricted recruitment caused the gradual decrease of Thomson's gazelle. Altogether, this confirms that the overall set-up of model was appropriate in depicting equivalent aspects of the Serengeti-Mara ecosystem.

9.3 Implications of the results

Following the construction and analysis of the present model, a number of hypotheses were drawn from the results. These could not only have far-reaching implications for the research that is undertaken in the Serengeti, but also on the future conservation of this area. The hypothesis that appears to be controversial in light of current opinions is that the migratory wildebeest population is being limited by the amount of grass available in the wet season on the plains. This opposes the generally accepted view that they are limited by dry season grass availability in their northern domain. Consequently, the majority of investigations have been conducted primarily with this in mind (Sinclair *et al.* 1985; Fryxell *et al.* 1988; Murray *et al.* 1992; Hilborn *et al.* 1995; Pascual & Hilborn 1995; Pascual *et al.* 1997). For example, Hilborn & Mangel's (1997) model to study migratory wildebeest population trends, with regard to their future conservation, solely focused on dry season grass availability in the northern Serengeti. Furthermore, Mduma *et al.* (1998, 1999) continue on a similar line of study, and acknowledge that they base their methodology on a long-term study by Sinclair (1974c, 1977a, 1979c). In this study, record high, dry season rainfall in 1971 was assumed to be directly responsible for migratory wildebeest and buffalo numbers increasing steeply. From this Sinclair proposed that migratory wildebeest and buffalo were regulated by dry season grass production. It is unfortunate that in the 40 years of research conducted in the Serengeti, there have been no studies to investigate the annual wet season grass production on the plains, so a comparison could have been made between the wet and the dry season. If the current model has proven anything at all, it is that in order to fully and accurately understand the dynamics of an ecosystem, research should not be biased and every option should be investigated whether or not it appears irrelevant. In this way, those aspects that prove to be immaterial to the overall dynamics can formally be eliminated.

In regard to the hypothesis drawn from the current model, concerning the factors other than grass availability that are potentially regulating herbivore populations, it is once again highlighted that there is a need for further field research. At present, very few studies have focused on any grazing herbivores in the Serengeti other than the migratory wildebeest, let alone those factors involved in regulating their populations (Sinclair 1974d; Sinclair & Norton-Griffiths 1982; East 1984; Senzota 1988; Borner *et al.* 1987). However, even these investigations have not produced any conclusive evidence to corroborate or dismiss any of the factors potentially regulating these herbivores. It is an understanding of such regulating factors that is undeniably essential in conserving these animals. Without this knowledge it is impossible to gain a complete idea of ecosystem function and thus formulate realistic management decisions. For instance, how do you prevent a herbivore population from decreasing when you do not know the reason why.

9.4 Future work on the model

It was intended from the beginning of this research that, although only the grazing dynamics of Serengeti-Mara ecosystem could be modelled within the scope of the thesis, the model would be designed to incorporate all the dynamics of the ecosystem. By establishing a foundation from which the construction of the model could be continued in the future, it was hoped that it would eventually become an essential tool in the conservation of the Serengeti. Consequently, if construction is to continue on the model, then there are some recommendations on the direction and progression of that work.

Initially, two aspects of the Serengeti were identified that could have potentially been modelled in this thesis. These included the grazing dynamics and browsing dynamics, from which, of course, the grazing sub-unit was chosen. Although, these are considered to be fairly separate from one another, the long-term changes in one can have significant consequences on the other. For example, a subject of particular concern at present is the effect of elephants on trees. Many believe that the isolation of a large elephant population within the Serengeti has led to an unsustainable level of tree destruction (Watson & Bell 1969; Croze 1974a, b; Pellew 1983; Spinage 1994; Hoare 2000). This is, in part, causing the progressive reduction of woodlands and subsequently, the expansion of grasslands (Watson & Bell 1969; Laws 1970; Croze 1974a, b; Cumming 1982; Pellew 1983; Dublin *et al.* 1990; Ruess & Halter 1990; Spinage 1994). By incorporating the browsing sub-unit into the model, the extent to which these habitats are changing can be investigated and corroborated further. It also includes two browsing species that are of high conservation priority in the Serengeti, the elephant and the black rhinoceros (Spinage 1973; Hillman 1979; Makacha *et al.* 1979; Douglas-Hamilton 1980; Poole & Thomsen 1989; Caughley *et al.* 1990; Leader-Williams 1990; Gakahu 1993; Burton 1994; Prins & van der Jeugd 1993; Sharp 1997; Walpole *et al.* 2001). Understanding the dynamics of these species may be vital for their future survival.

With the majority of herbivores included in the model, the next stage would be to fully incorporate carnivores. At present only the effects of five large carnivore species on grazing herbivores have been included. This work has created a convenient framework from which survival and recruitment curves for each species can be created. Their inclusion in the model, may reveal the factors regulating their populations, such as illegal hunting, disease, interspecific competition, social organisation; herbivore populations or combination of these. Many studies have already attempted to investigate these factors, as carnivore conservation is a primary issue, not just in the Serengeti-Mara ecosystem, but throughout Africa (Hofer *et al.* 1993; Burrows 1995; Laurenson 1995; Nowell & Jackson 1996; Woodroffe *et al.* 1997; Mills & Hofer 1998; Vutcetich & Creel 1999). Therefore, modelling the carnivore populations in the Serengeti, will amalgamate the data that has been collected and hopefully increase our understanding of their dynamics, so that essential conservation management decisions can be made as soon as possible.

9.5 Implications for conservation

At present, limited size, insularisation, isolation, edge effects, disease transmission from domestic animals, the impact of introduced species, global climatic changes, pollution, poaching and many other factors threaten the viability of biodiversity in all the remaining natural areas in the world (MacArthur & Wilson 1967; Terborgh 1974; Western & Gichohi 1993). It is now very apparent that in order to ensure the survival of the fauna and habitats these areas contain, more active conservation measures need to be taken. However, in order to define, plan and implement an appropriate action, good knowledge and understanding of ecosystem function is required. For instance, an anomalous change in just one component can trigger a disturbance cascade through the entire ecosystem, leading to a progressive loss of species diversity and habitat heterogeneity (McNaughton 1989; Walker 1989).

Researchers in the Serengeti-Mara ecosystem have been working towards increasing their knowledge of this diverse area since 1960, and in the process have accumulated a great deal of information (Lamprey *et al.* 1971). Nevertheless, even after 40 years of research there has been limited progress made in advancing our understanding of how this ecosystem functions. Consequently, much needed active conservation can still not be implemented because of the unknown probability of inadvertently changing the ecological regime of the Serengeti in the process. By constructing a theoretical ecosystem model, such as that initiated in this thesis, a greater understanding of the dynamics of the Serengeti can be achieved. It acts as an analytical tool, amalgamating available data, examining the complex combination of processes governing the ecosystem and exposing gaps in our knowledge. Furthermore, it can be used forecast population dynamics under current conditions, as well as predicting the affects of various active management strategies and subsequently identifying the most effective to preserve the ecosystem.

The current model, even in its initial stages, has already demonstrated not only that our understanding of the dynamics of the Serengeti can be increased substantially by constructing such a model, but also that it reveals the direction in which future research should be proceeding. This information is particularly important, as both time and available funding inevitably limit research and therefore the conservation of the area. Of course, the model's proficiency at identifying effective management strategies is still yet to be determined, but these capabilities will doubtless be essential in defining, planning and implementing appropriate strategies for the long-term conservation of the Serengeti-Mara ecosystem and potentially other similar ecosystems across Africa.

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Table 1 Manipulated annual fire percentage for the three zones in the Serengeti-Mara ecosystem from Norton-Griffiths (1979) in black; and red values with help from Dublin (1986) and Dublin *et al.* (1990).

	Percentage area burn in the dry season		
Year	Zone 1	Zone 2	Zone 3
1960	100	85	52
1961	100	85	52
1962	100	85	52
1963	98	81	48
1964	95	77	46
1965	91	74	42
1966	85	71	38
1967	80	67	34
1968	74	64	29
1969	70	60	26
1970	66	56	23
1971	60	51	20
1972	55	48	18
1973	51	45	14
1974	45	41	12
1975	40	38	10
1976	35	35	8
1977	30	31	6
1978	25	28	4
1979	20	25	2
1980	10	21	2
1981	5	18	2
1982	5	15	2
1983	5	11	2
1984	5	8	2
1985	5	5	2
1986	5	5	2
1987	5	5	2
1988	5	5	2
1989	5	5	2

Table 2 Hayssen & Lacy's (1985) coefficients estimated from the log linear relationship between metabolic rate and body size for a number of different mammalian taxa.

Taxon	N	a	(SE)	b	(SE)	R^2
Class Mammalia	293	0.636	0.027	-0.307	0.011	0.748
Subclass Prototheria	3	1.431	0.702	-0.621	0.194	0.911
Subclass Theria	290	0.630	0.027	-0.303	0.010	0.747
Infraclass Metatheria	42	0.397	0.036	-0.253	0.013	0.906
Infraclass Eutheria	248	0.649	0.029	-0.304	0.011	0.740
Order Afrosoricida Order Eulipotyphla	26	1.195	0.085	-0.582	0.044	0.878
Order Chiroptera	35	0.561	0.086	-0.286	0.055	0.545
Order Primates	10	0.423	0.267	-0.245	0.098	0.436
Order Xenarthra Order Pholidota	13	0.502	0.190	-0.344	0.052	0.800
Order Lagomorpha	6	0.843	0.263	-0.332	0.085	0.794
Order Rodentia	122	0.697	0.043	-0.331	0.021	0.668
Order Carnivora	18	0.630	0.177	-0.262	0.050	0.628
Order Artiodactyla	12	0.396	0.285	-0.198	0.060	0.520

Table 3 Proportional distribution of wildebeest amongst 24 different weight classes under a normal distribution.

Z value at each class limit	Proportional distribution from Z value	Proportional distribution of each weight class
-3	-0.0013	0.0017
-2.75	-0.003	0.0032
-2.5	-0.0062	0.006
-2.25	-0.0122	0.0106
-2	-0.0228	0.0173
-1.75	-0.0401	0.0267
-1.5	-0.0668	0.0388
-1.25	-0.1056	0.0531
-1	-0.1587	0.0679
-0.75	-0.2266	0.0819
-0.5	-0.3085	0.0928
-0.25	-0.4013	0.0987
0	0.5	
0.25	0.4013	0.0987
0.5	0.3085	0.0928
0.75	0.2266	0.0819
1	0.1587	0.0679
1.25	0.1056	0.0531
1.5	0.0668	0.0388
1.75	0.0401	0.0267
2	0.0228	0.0173
2.25	0.0122	0.0106
2.5	0.0062	0.006
2.75	0.003	0.0032
3	0.0013	0.0017

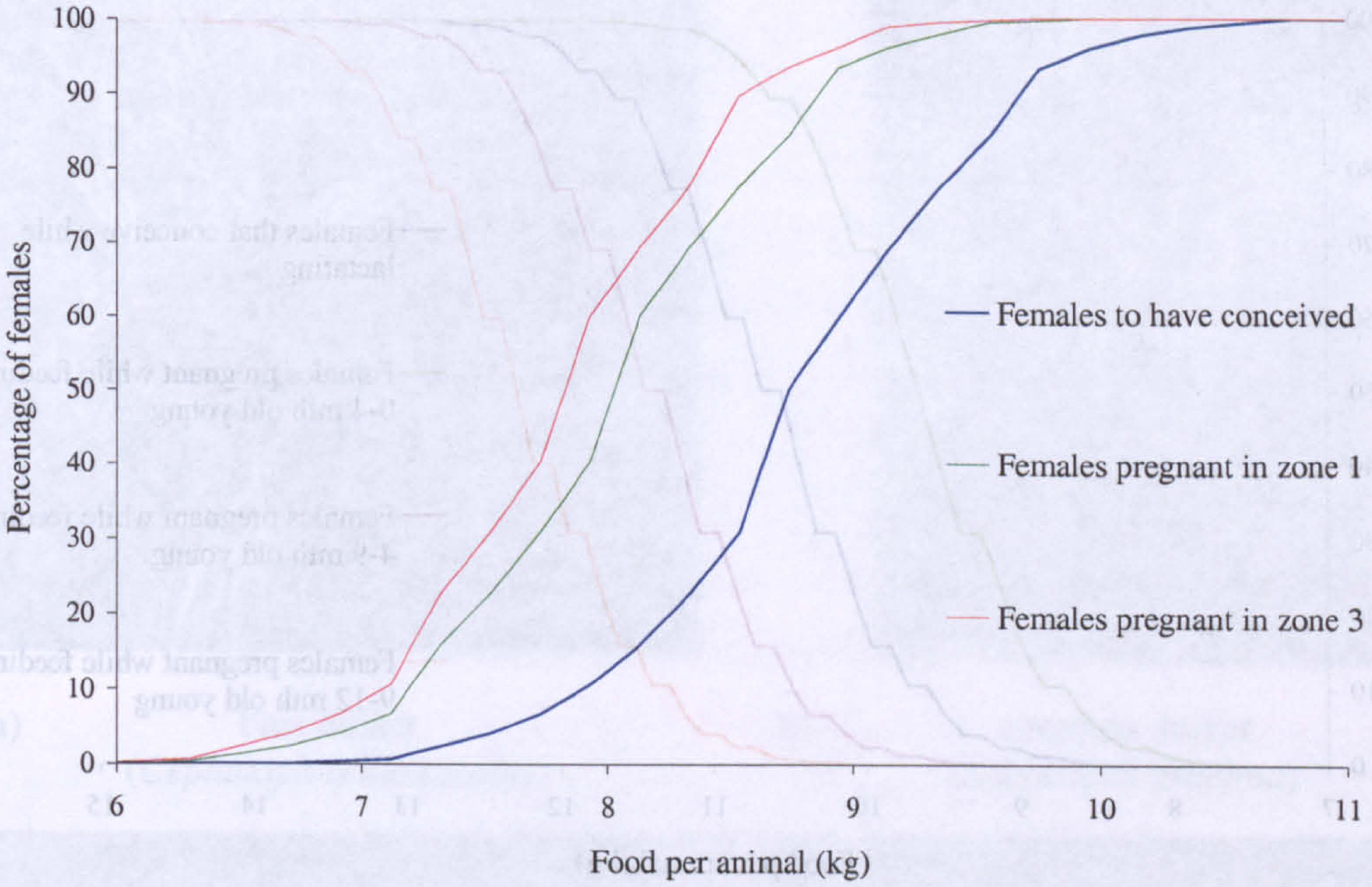

Figure 1 Relationship between food availability and the conception and pregnancy of females.

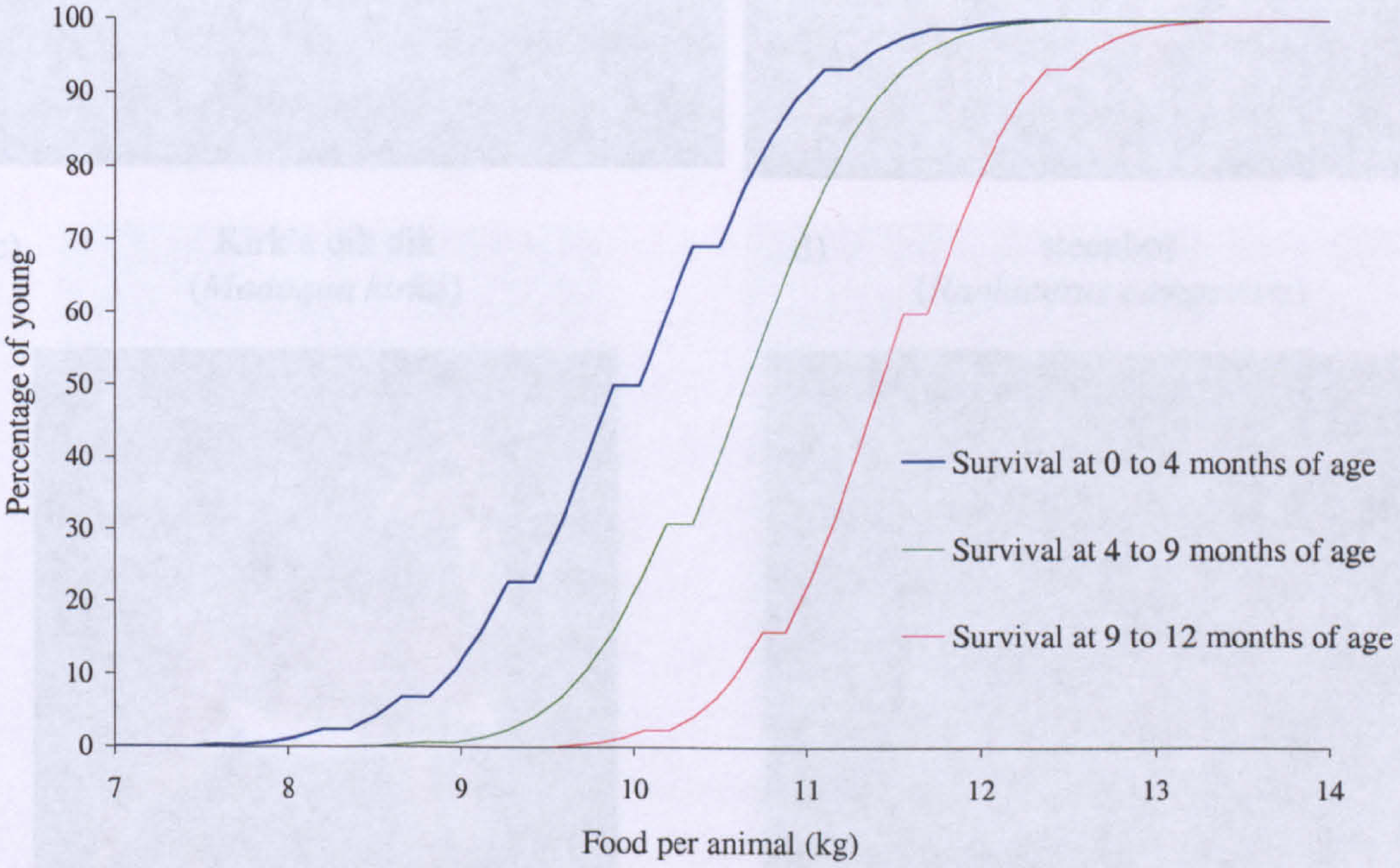

Figure 2 Relationship between food availability and young aged 0 to 4 months, 4 to 9 months and 9 to 12 months.

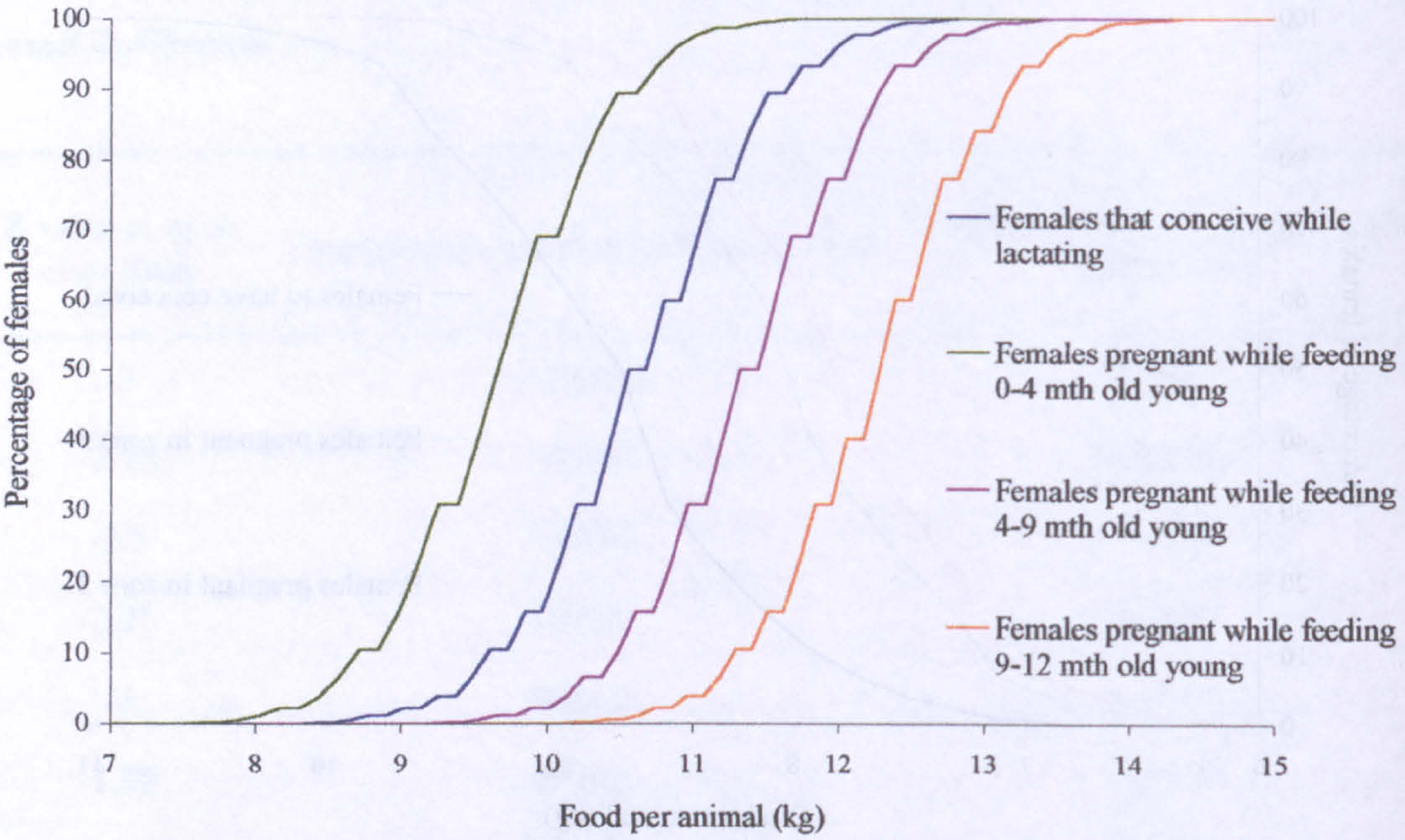

Figure 3 Relationship between FpA and females conceiving and maintaining their pregnancy while feeding growing offspring.


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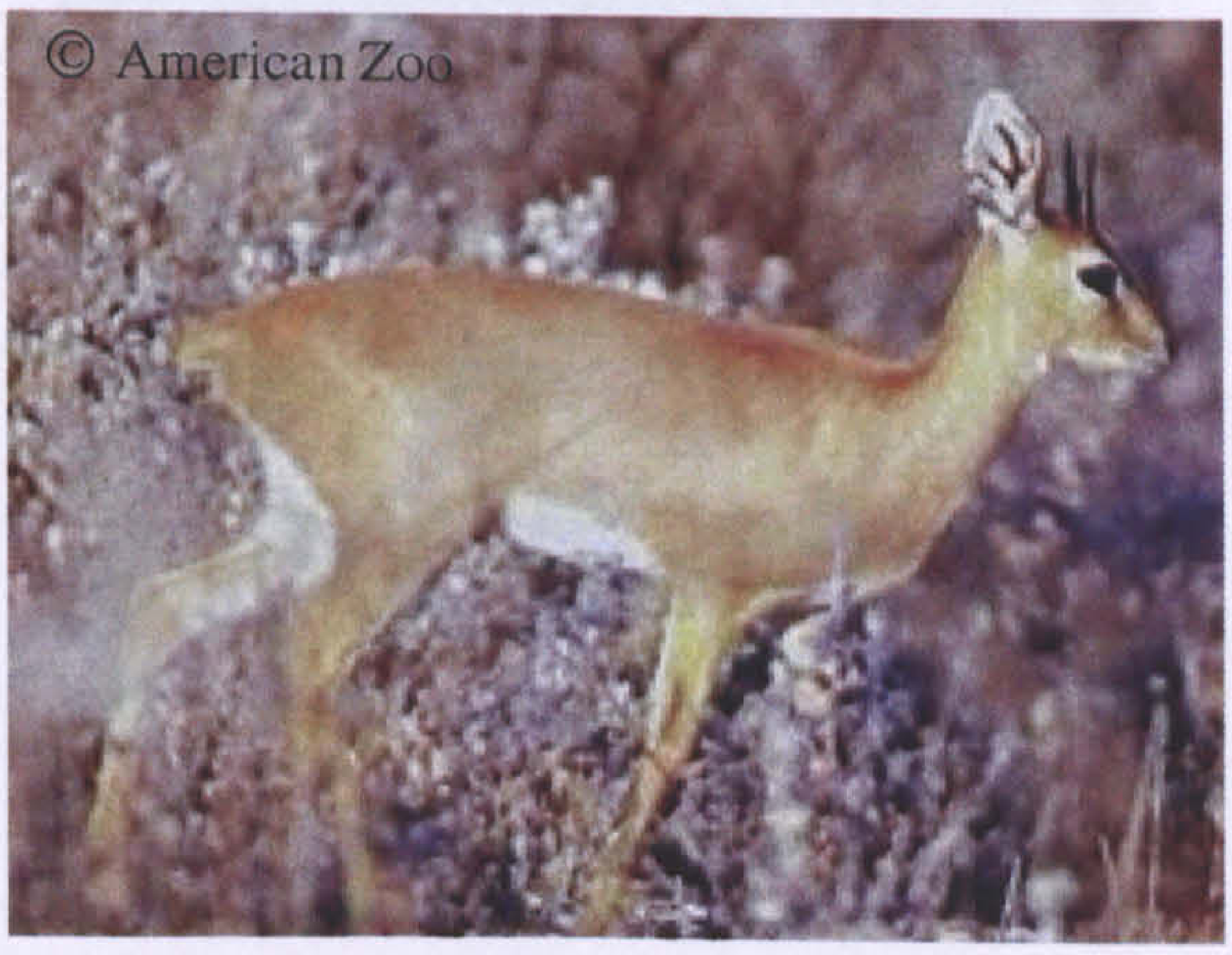
a) blue duiker
(*Cephalophus monticola*)


© Brent Huffman

b) common duiker
(*Sylvicapra grimmia*)


© Tory Bennett

c) Kirk's dik dik
(*Madoqua kirkii*)


© American Zoo

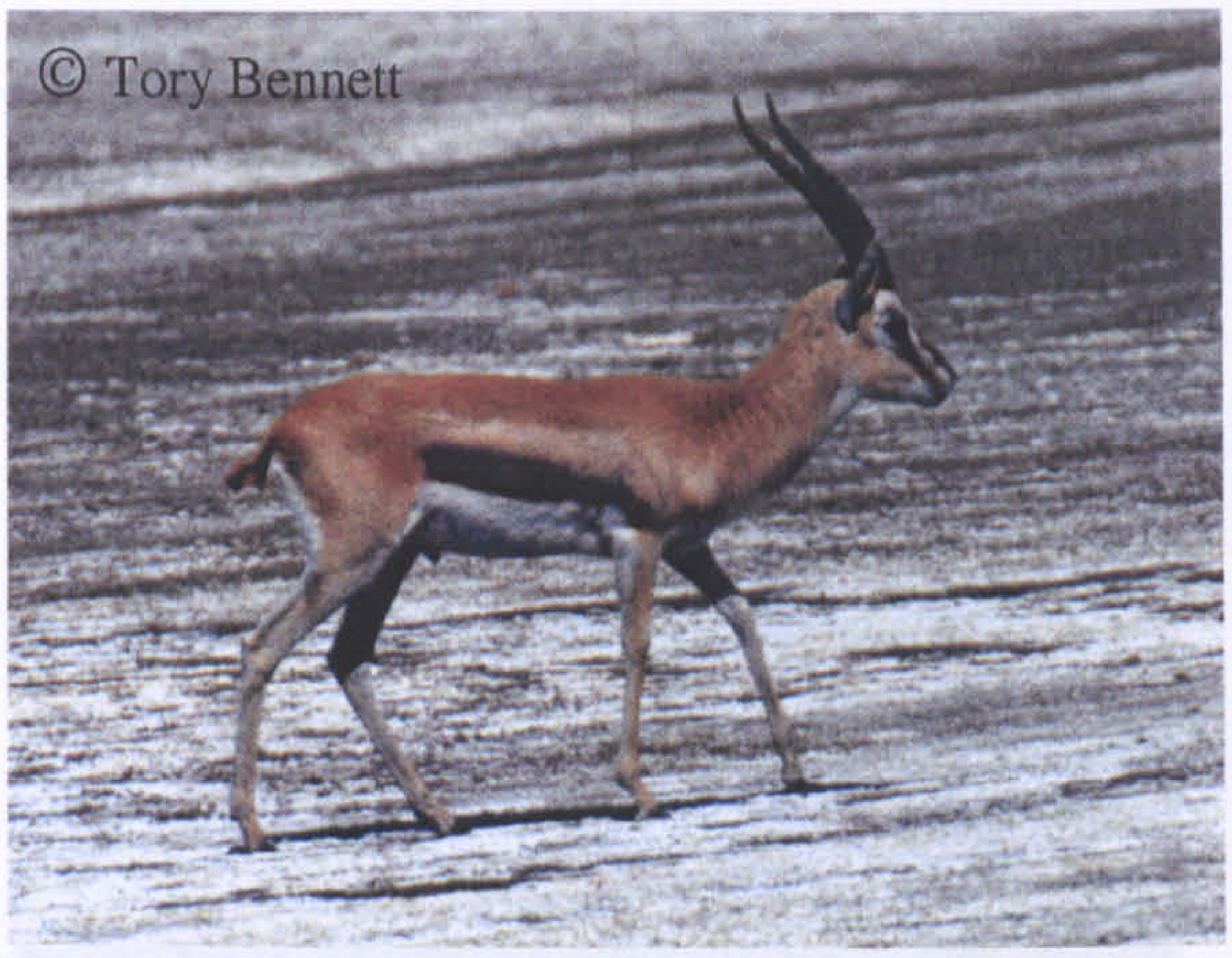
d) steenbok
(*Raphicerus campestris*)


© American Zoo

e) oribi
(*Ourebia ourebi*)


© Ralf Schmode

f) klipspringer
(*Oreotragus oreotragus*)


© Tory Bennett

a) Thomson's gazelle
(*Gazella thomsonii*)


© Tory Bennett

b) Grant's gazelle
(*Gazella granti*)


© Eric van Poppel & Caroline Don

c) Bohor reedbuck
(*Redunca redunca*)


© Tory Bennett

d) Defassa waterbuck
(*Kobus ellipsiprymnus defassa*)


© American Zoo

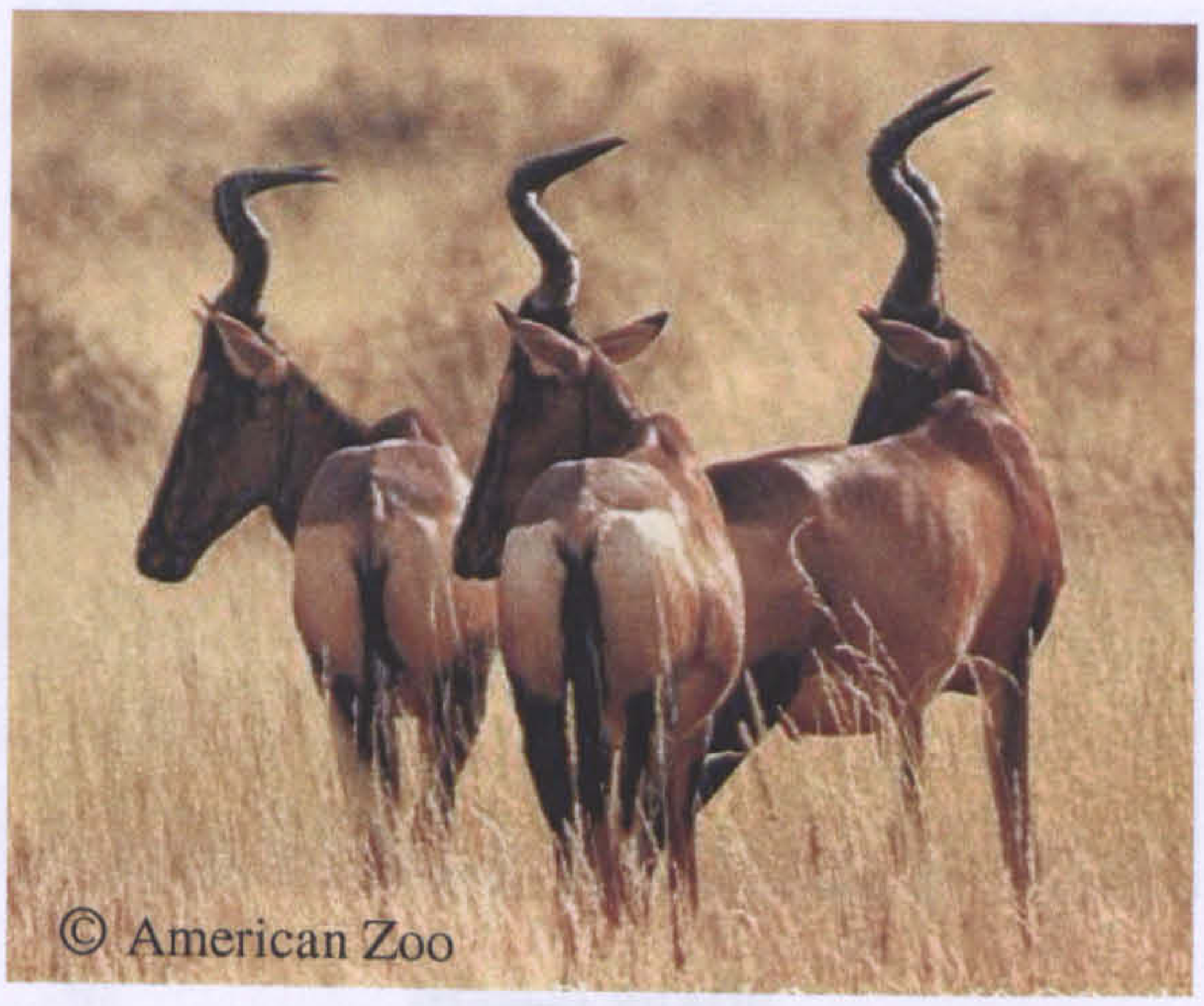
e) roan
(*Hippotragus equinus*)


© American Zoo

f) Fringe-eared oryx
(*Oryx gazella callotis*)


© South African Tourism

a) wildebeest
(*Connochaetes taurinus*)


© American Zoo

b) Coke's hartebeest
(*Alcelaphus buselaphus cokii*)


© South African Tourism

c) topi
(*Damaliscus lunatus*)


© Brent Huffman

d) common eland
(*Taurotragus oryx*)


© American Zoo

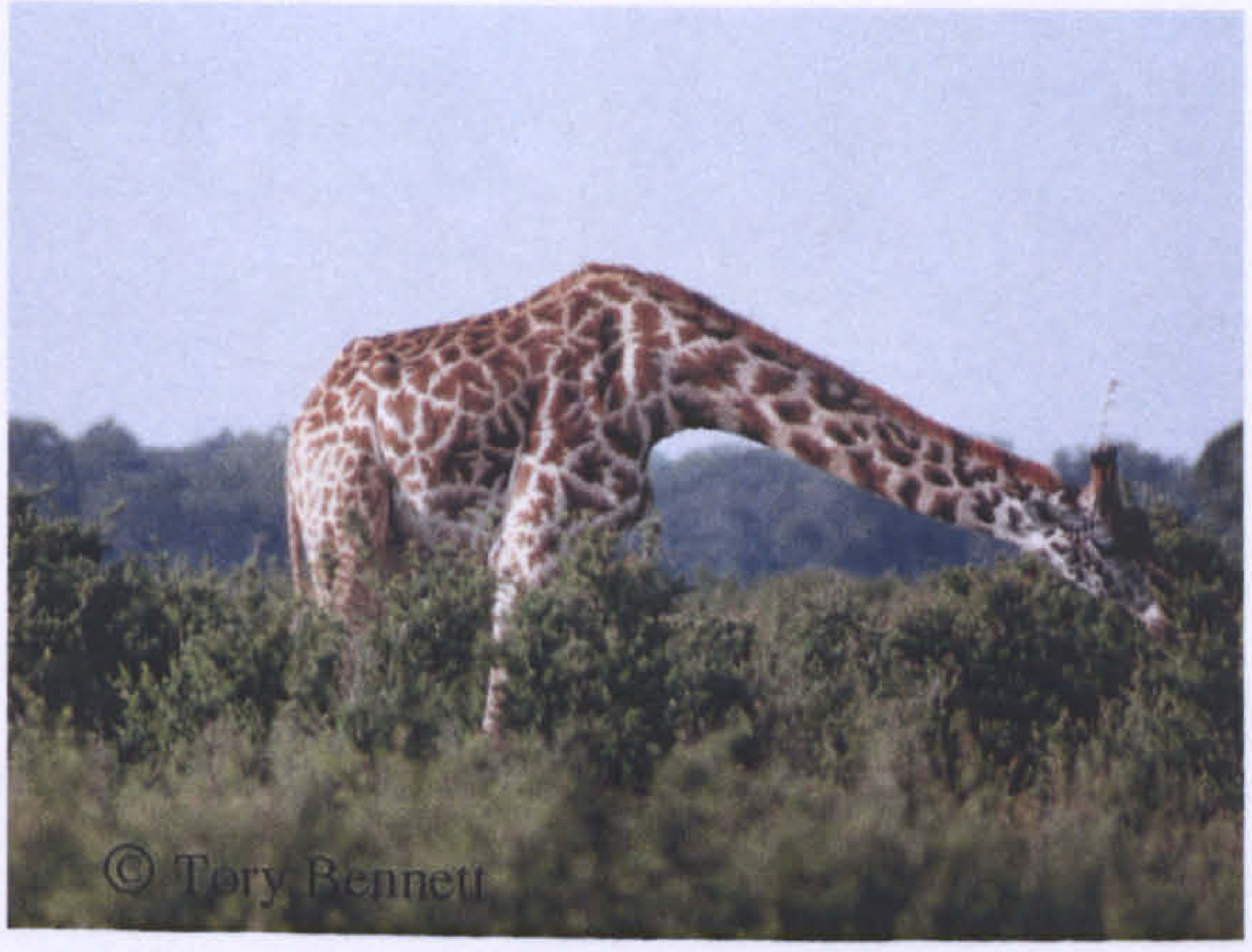
e) bushbuck
(*Tragelaphus scriptus*)


© Tory Bennett

f) African buffalo
(*Syncerus caffer*)


© Tory Bennett

a) impala
(*Aepyceros melampus*)


© Tory Bennett

b) Maasai giraffe
(*Giraffa camelopardalis tippelskirchi*)


©Brent Huffman

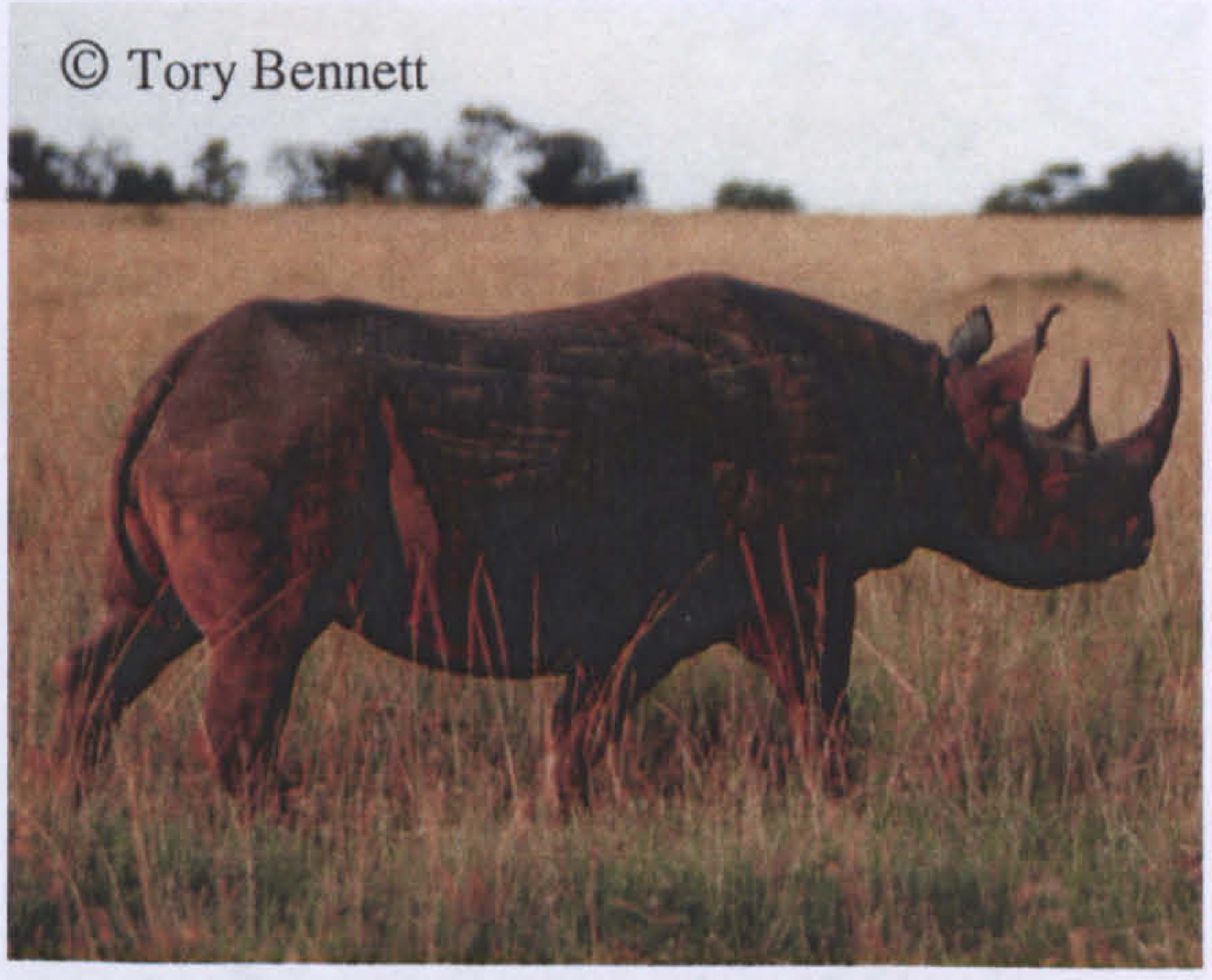
c) hippopotamus
(*Hippopotamus amphibius*)


© American Zoo

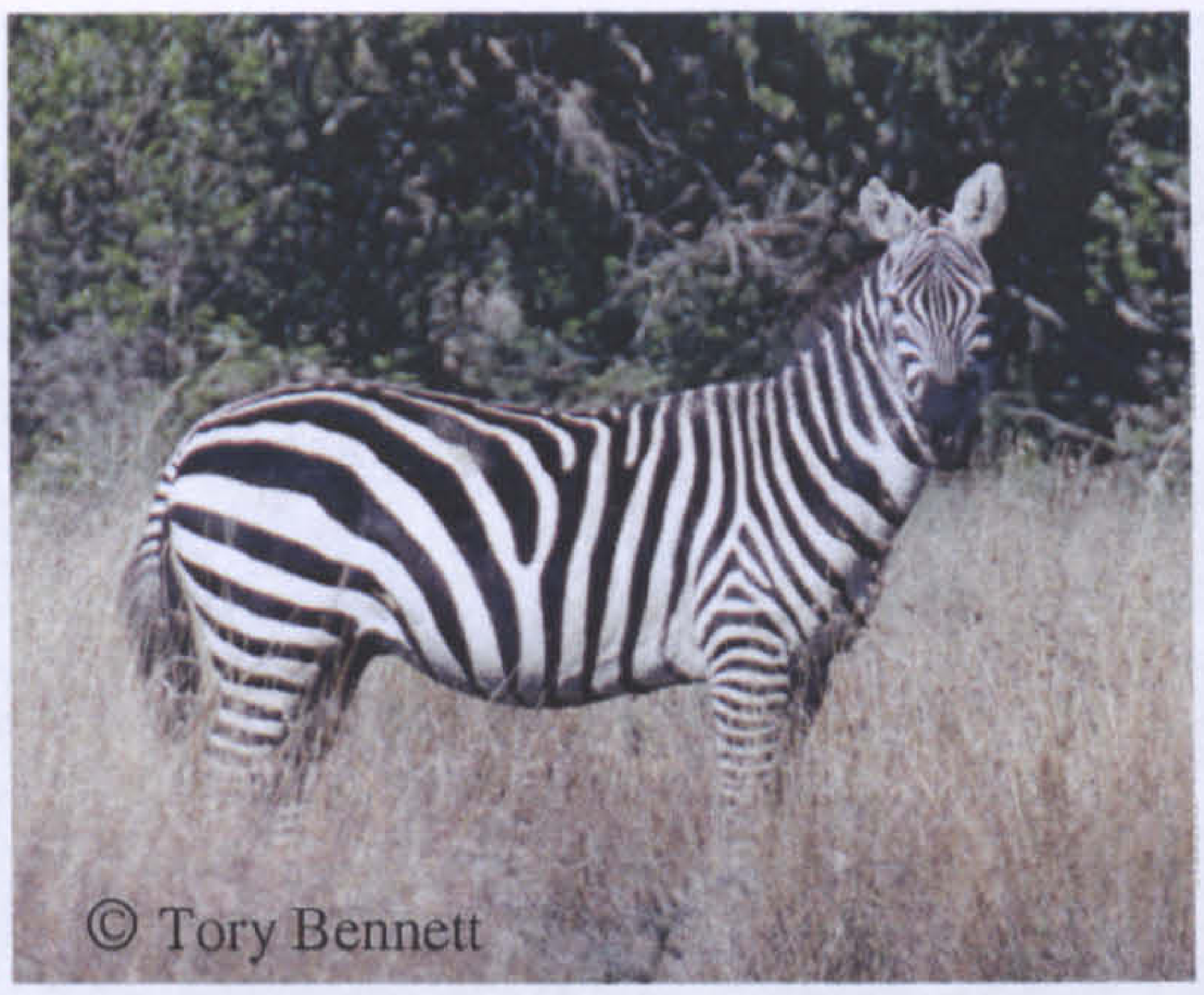
d) bushpig
(*Potamochoerus larvatus*)


© Tory Bennett

e) common warthog
(*Phacochoerus africanus*)

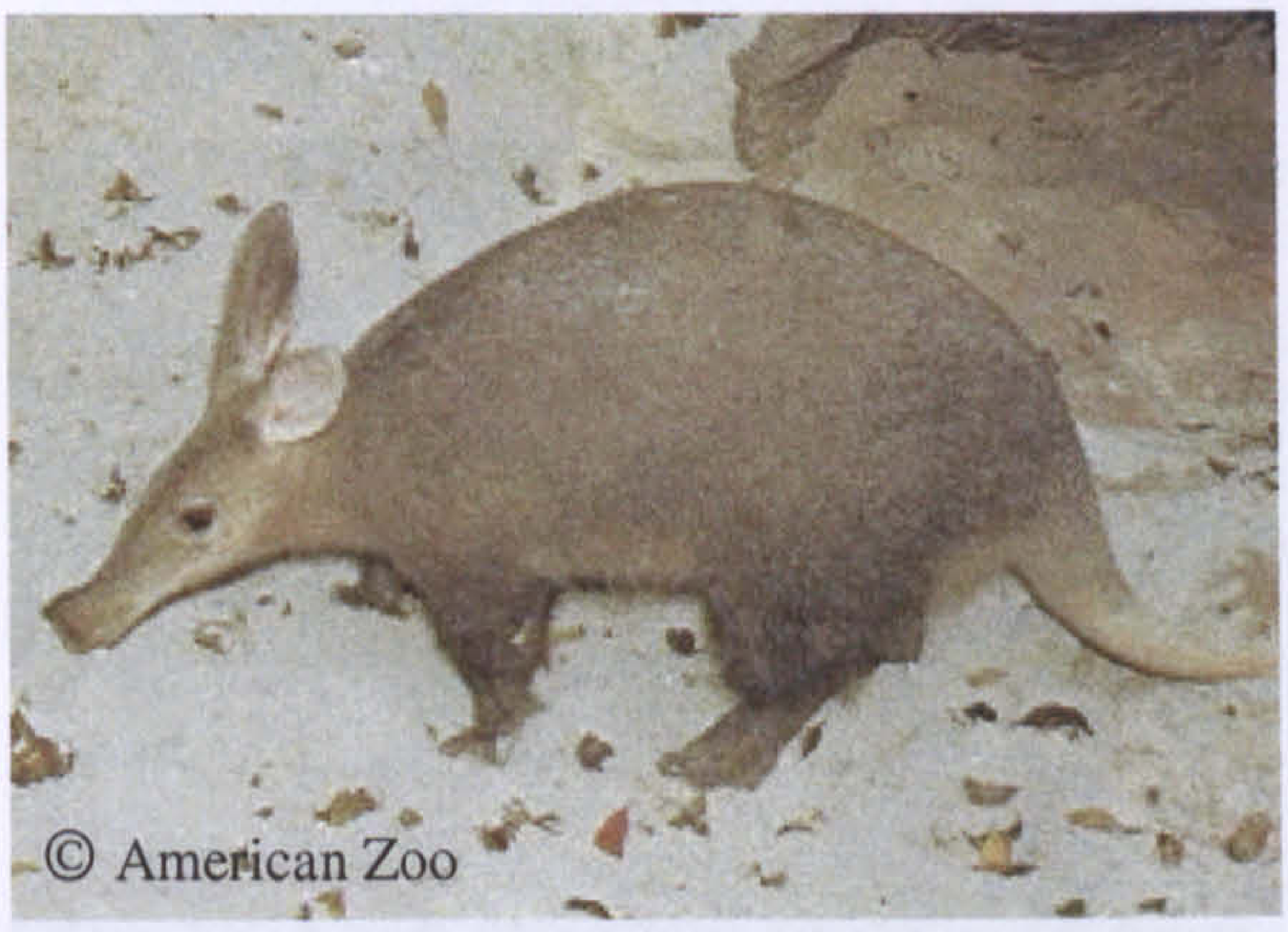

© Tory Bennett

f) black rhinoceros
(*Diceros bicornis*)



a) Burchell's zebra
(*Equus burchellii*)

b) elephant
(*Loxodonta africana*)



c) aardvark
(*Orycteropus afer*)

d) rock hyrax
(*Procavia johnstoni*)

e) bush hyrax
(*Heterohyrax brucei*)

f) African civet
(*Civettictis civetta*)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a) common genet
(*Genetta genetta*)


© American Zoo

b) African palm civet
(*Nandinia binotata*)


© American Zoo

c) marsh mongoose
(*Atilax paludinosus*)


© American Zoo

d) Egyptian mongoose
(*Herpestes ichneumon*)


© Safaricamlive

e) slender mongoose
(*Herpestes* (*Galerella*) *sanguineus*)


© Eric & David Hosking

f) dwarf mongoose
(*Helogale parvula*)

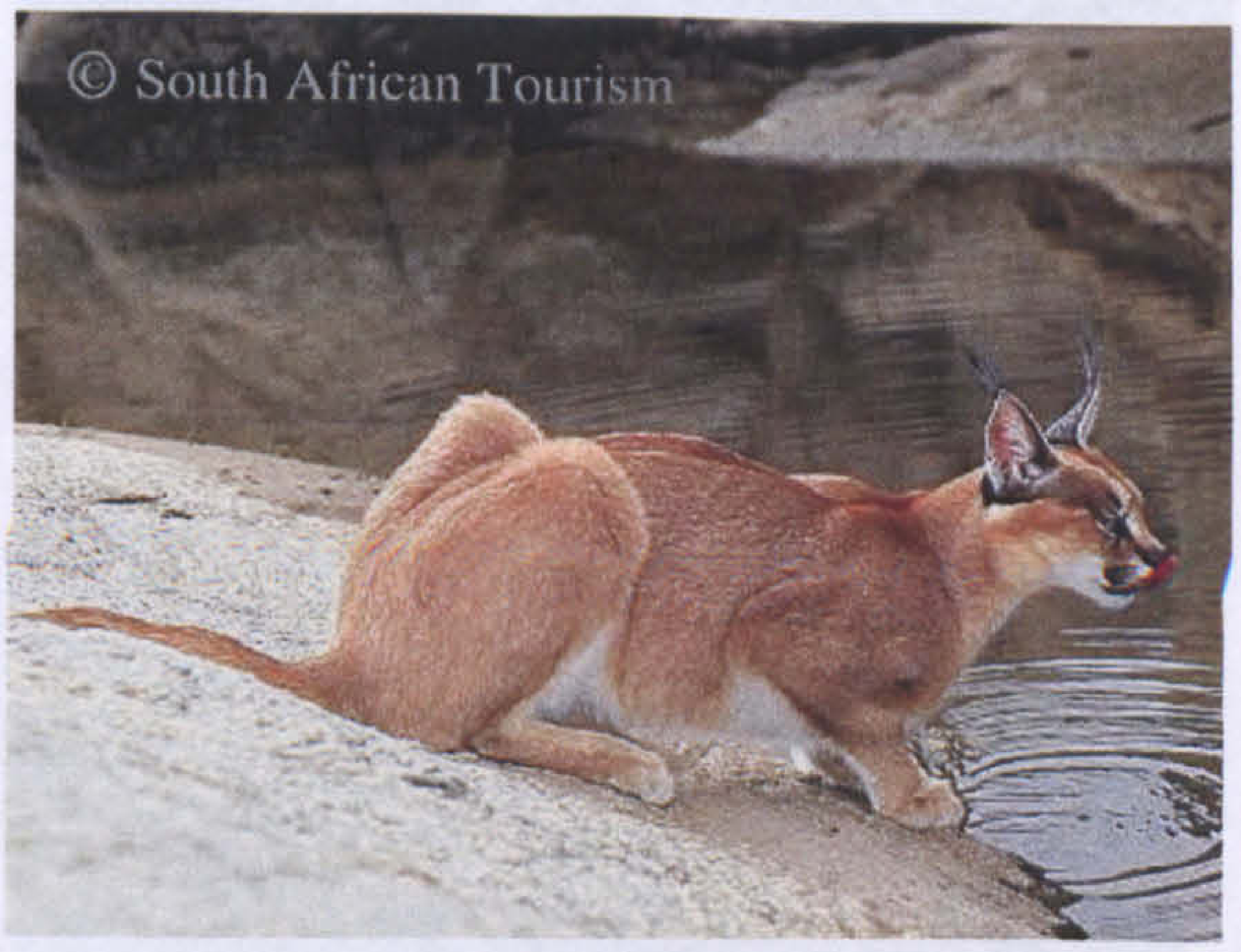
a) banded mongoose
(*Mungos mungo*)

b) white-tailed mongoose
(*Ichneumia albicauda*)

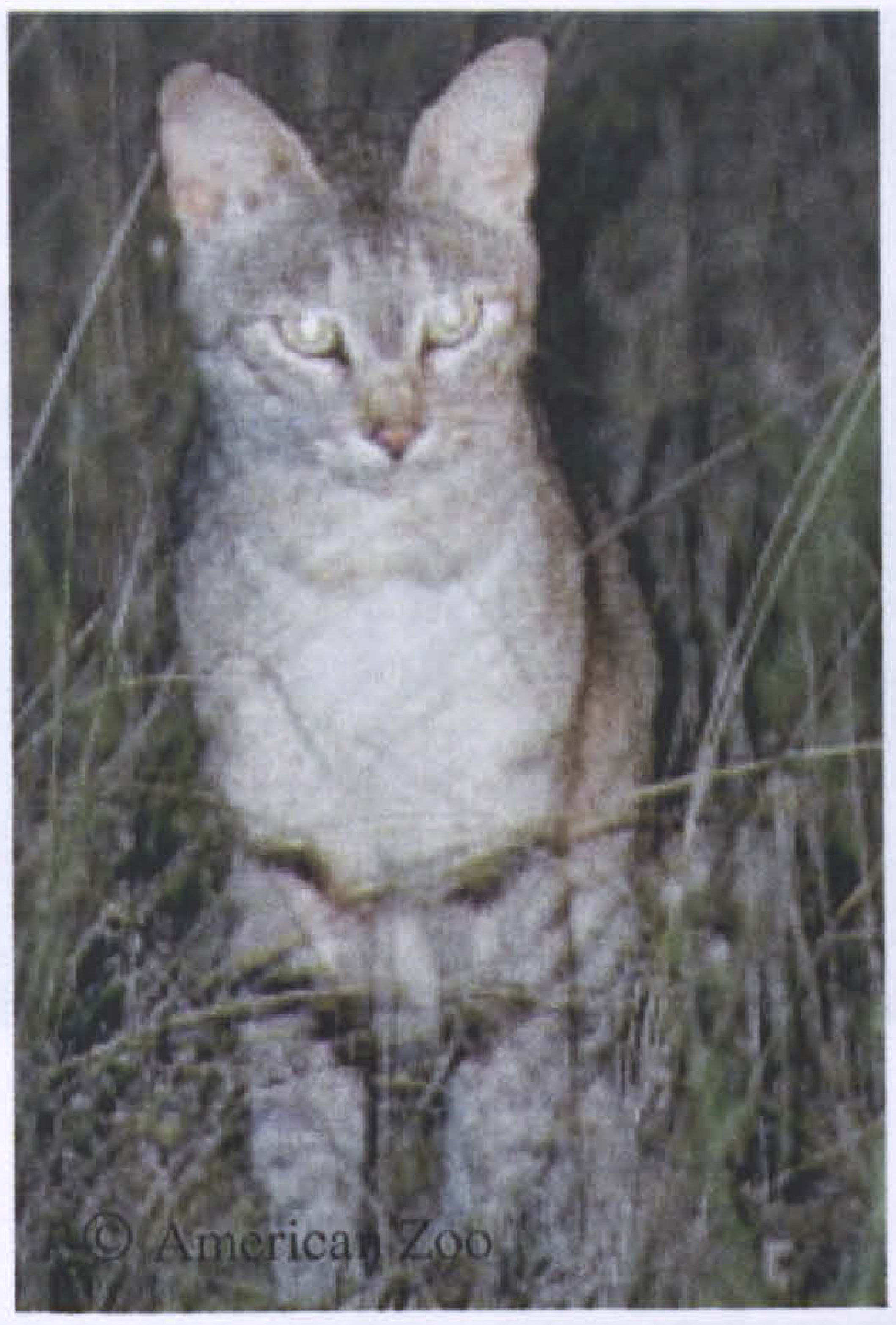
c) lion
(*Panthera leo*)

d) leopard
(*Panthera pardus*)

e) cheetah
(*Acinonyx jubatus*)

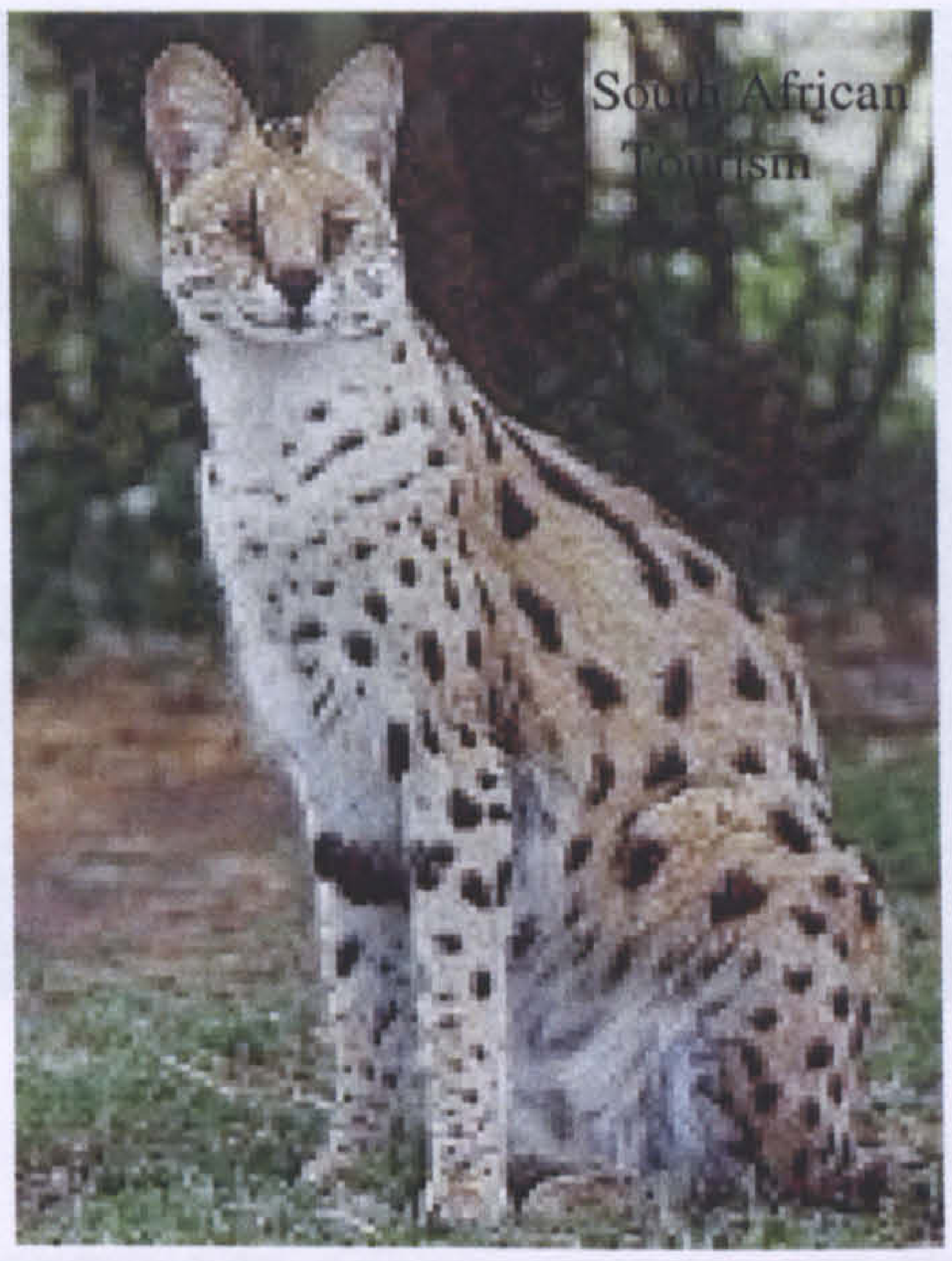


f) caracal
(*Felis* (*Caracal*) *caracal*)



© American Zoo

a) African wild cat
(*Felis silvestris lybica*)



© South African Tourism

b) serval
(*Felis* (*Leptailurus*) *serval*)

© American Zoo

c) bat-eared fox
(*Otocyon megalotis*)

© South African Tourism

d) golden jackal
(*Canis aureus*)

© Gallo Images

e) side-striped jackal
(*Canis adustus*)

© Tory Bennett

f) black-backed jackal
(*Canis mesomelas*)


© American Zoo

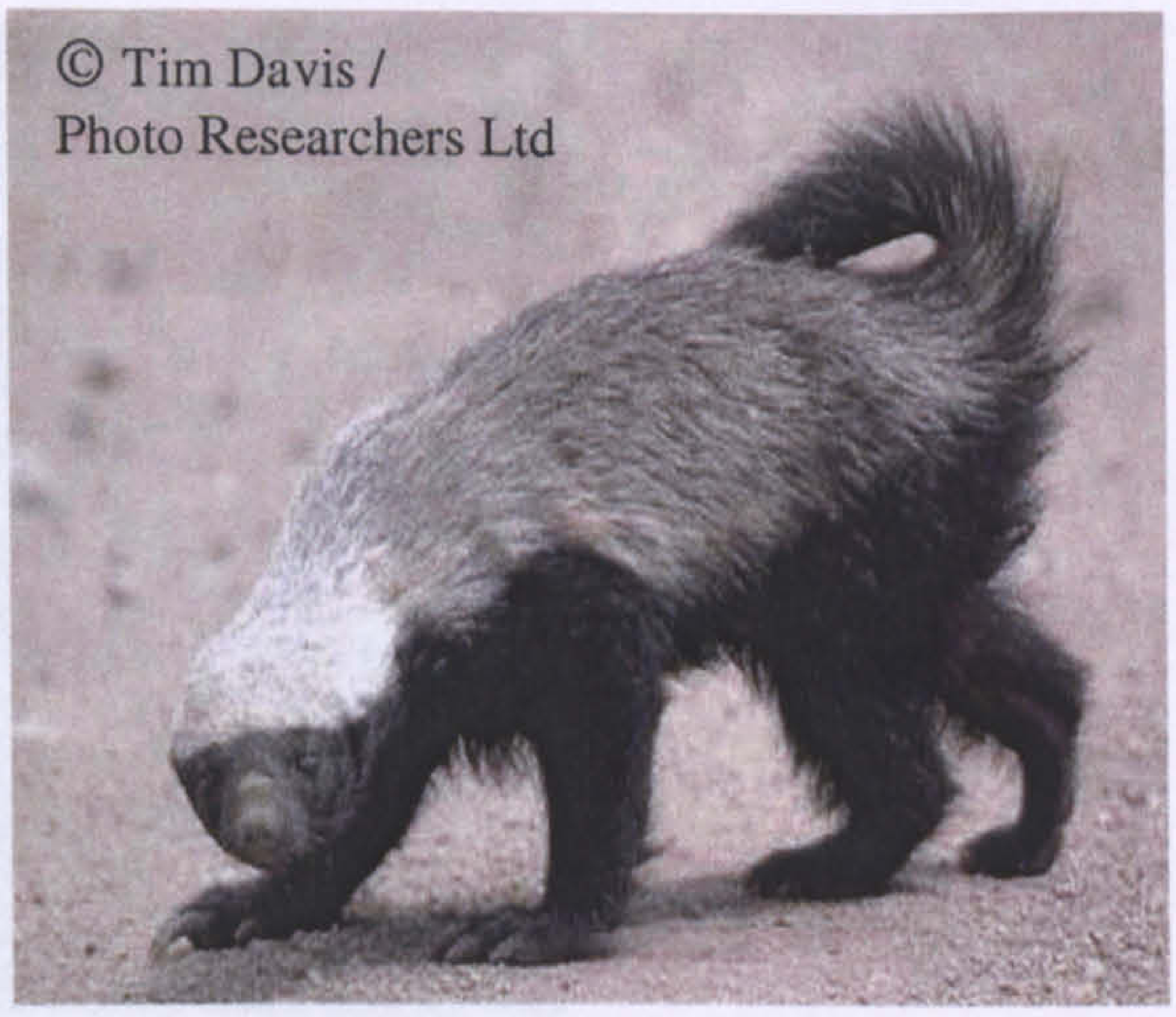
a) African hunting dog (*Lycaon pictus*).


© American Zoo

b) Cape clawless otter (*Aonyx capensis*)


© Allen Matheson

c) spot-necked otter (*Lutra maculicollis*)


© Tim Davis / Photo Researchers Ltd

d) honey badger (*Mellivora capensis*)


© American Zoo

e) zorilla (*Ictonyx striatus*)


© Stuart & Stuart

f) African striped weasel (*Poecilogale albinucha*)

© J. van Wormer

a) striped hyaena
(*Hyaena hyaena*)

© American Zoo

b) spotted hyaena
(*Crocuta crocuta*)

© American Zoo

c) aardwolf
(*Proteles cristatus*)