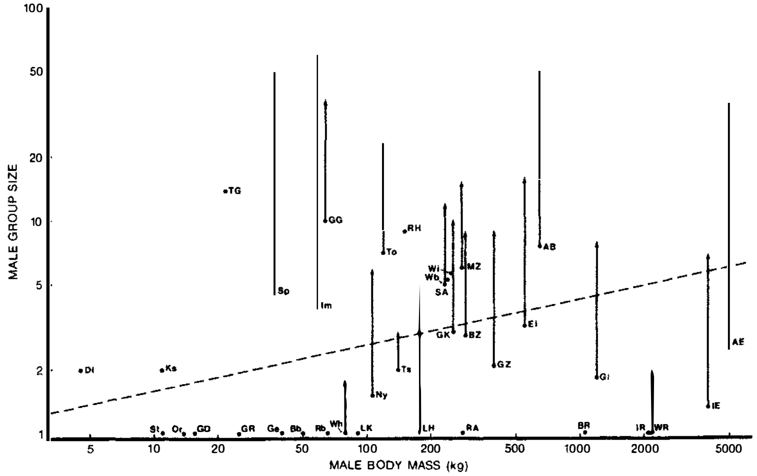

Fig. 9.3 Male group sizes of African large herbivores in relation to body mass. Dots indicate the mean size of all-male groups, arrow the maximum recorded group size. Key to species labels given in Appendix I, references as in Fig. 9.2.

Regression excluding megaherbivores (dashed line, based on means): $MALGP = 0.96M^{0.21}$ ($R^2 = 0.11$, $N = 30$, $0.1 > P > 0.05$). Including megaherbivores no correlation results.

The temporary associations among elephant males seem to be related mainly to the establishment and maintenance of dominance rankings among individuals sharing a common home region. Maintenance of extended social relationships could be a factor in the amalgamation of different family units of elephants, but this does not explain the formation of the cohesive family units.

Other factors besides predation risks to be considered include:

(a) *Habitat structure.* Populations in open habitats tend to form larger groups than populations in closed habitats. This is promoted both proximally, because it is easier for animals to maintain contact where visibility range is high, and ultimately, because predator detection benefits are greater. Notably, browsers occupying wooded habitats, such as tragelaphine antelope species, tend to form smaller groups than grazers of similar body mass (Fig. 9.2). However, this factor would not explain the differences in group size between white rhinos, which are open savanna grazers, and elephants, which are mixed feeders occupying a range of habitats from forests to open savanna woodlands.

(b) *Mobility.* For animals wandering over extensive home ranges, there are potential advantages for younger individuals to remain attached to older ones in order to gain from the experience of the latter regarding the

population densities are low. Thus encounters between equally powerful rival males are rare enough for a strict assertion of spatial dominance to be unnecessary. Nevertheless territoriality is clearly expressed in the high density population (nearly 1 per km^2) of black rhinos in the Hluhluwe Reserve, and there is suggestive evidence of its existence even in the relatively sparse black rhino population inhabiting the Namib Desert fringe. White rhinos and hippos, which commonly occur in densities exceeding 1 per km^2, exhibit territorial dominance systems similar in form to those typical of many savanna antelope species.

Both African and Asian elephants tend to aggregate in large herds during the breeding season. Because of the mobility of female groups, a territorial restriction by males would not be advantageous. Thus an individually based rank dominance system similar to that of African buffalo would theoretically be predicted. Elephants do indeed show fairly stable dominance rankings, but superimposed on this is the temporal restriction on dominance imposed by musth periods. It seems that the reduction in contesting brought about by a rank dominance system alone is inadequate.

The survival costs associated with alternative male dominance systems are indicated by the surplus mortality that adult males experience relative to females. This was estimated to be an extra 2% per annum for white rhino bulls, and 3.8% per annum for black rhino bulls (Chapter 8). Notably, for both of these species over half of male deaths could be ascribed to injuries sustained in fights. The surplus mortality incurred by African elephant bulls relative to cows appears to be less than 2% per annum, but this estimate is derived from comparing mortality rates in two different populations. Furthermore, half of the mortality was inflicted by human hunting, which falls more heavily on males than on females.

Among north temperate ungulates, where territorial restrictions are generally lacking, considerably higher mortality costs are shown by males. Rutting injuries accounted for an annual mortality of 10% in Rocky Mountain goats, and 4% in moose. For bighorn sheep the annual mortality rate of males rose from 4% to 16% per annum on attainment of prime breeding age at 8 years (Geist 1971). For greater kudu, a non-territorial African antelope, the annual mortality rate of prime-aged males exceeded 50% per annum, compared with 7% per annum for prime-aged females. However, this surplus male mortality seemed to be a result of the indirect costs associated with increased male body size relative to females, rather than due directly to fighting injuries (Owen-Smith 1984, in preparation). At the other extreme, in African buffalo the annual mortality rate of prime-aged bulls exceeds that of prime-aged females by less than 1% (Sinclair

claim territorial dominance must either emigrate to peripheral less contested regions, where there are fewer females; or remain on in a more favorable region, temporarily foregoing reproductive opportunities while awaiting an opportunity to claim a territory. Both of these tactics are exhibited by white rhino bulls; but the tactic of wandering from one territory to another, as shown by bachelor males in some antelope species, is too risky and is restricted to short transitional periods. Hippo bulls are restricted by the availability of suitable refuge pools, with subdominant males dispersing into small pools when these are available (Laws & Clough 1966).

Mating gains

Many workers have related territoriality to defense of the food resources contained within territories, serving either to promote the survival of territory holders, or, in the case of male-only territories, to attract females by monopolizing sites of resource enrichment (e.g. Brown & Orians 1970; Emlen & Oring 1977). Owen-Smith (1977) suggested that territoriality among ungulates is promoted by intrasexual selection among males competing for mating opportunities. He suggested that the strength of such sexual selection could be estimated in terms of the 'Potential Mating Enhancement Factor', better termed the 'Potential Seasonal Mating Enhancement' (PSME). This was defined as the annual number of matings achieved by the most successful male in a local population of competing males, relative to the sex ratio of fertile females to potent males. He suggested further that the ultimate effects on fitness are indicated by the 'Potential Lifetime Mating Enhancement' (PLME). This is calculated by integrating seasonal mating performances over the reproductive lifespan, and dividing by the maximum lifetime reproductive output expected for a female. A PLME significantly greater than unity indicates that the variance in male reproductive output is greater than that for females, i.e. there is effective scope for intrasexual selection among males.

It has been assumed by many authors, from Darwin (1871) to Georgiadis (1985), that the degree of body size dimorphism between the sexes reflects the strength of sexual selection operating in a species. Wiley (1974) noted for grouse (Tetraonidae) that delayed sexual maturation by males is a feature of larger species, and that this automatically leads to strong sexual selection because of its consequences for the functional sex ratio. Ralls (1977), comparing birds and mammals, suggested that there was a predictable relation between extreme polygyny and extreme sexual dimorphism, but cautioned that sexual selection could not account for all of the observed

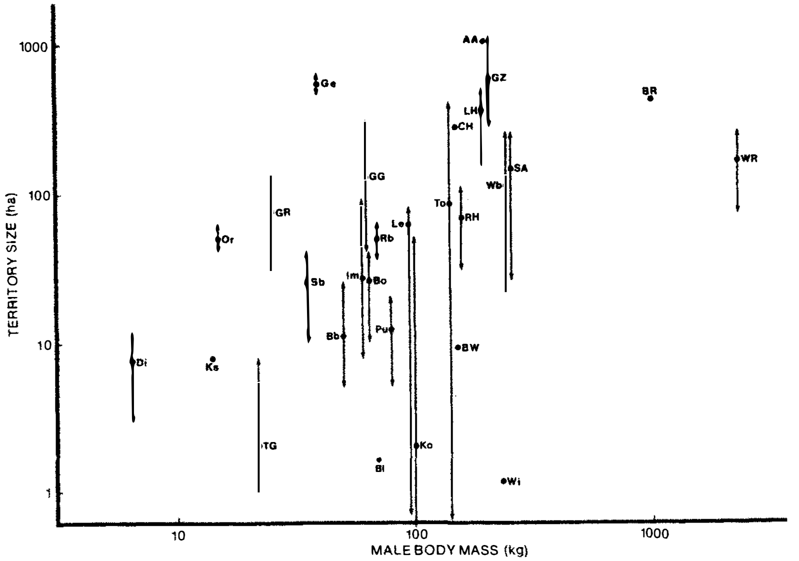

Fig. 9.4 Male territory sizes of ungulates in relation to body mass. The mean and range of territory sizes reported are shown. Key to species labels given in Appendix I. Data from David (1978), Duncan (1975), Murray (1982a), Oliver *et al.* (1978), Owen-Smith (1977).

Regression line (based on means): TER (ha) $= 2.63M^{0.63}$ (SE(b) $= 0.258$, $R^2 = 0.18$, $N = 30$, $P = 0.021$).

variability among species. Clutton-Brock *el al.* (1977) found for primates that, if monogamous species were excluded, there was no correlation between size dimorphism and degree of polygyny, as measured by the socionomic sex ratio. Instead there was a positive correlation between size dimorphism and body mass. Reiss (1986) suggests that the main reason for the association between size and sexual dimorphism is because factors such as food distribution influence both size and opportunities for polygyny.

If the function of a territory was to hold a population of potential mates, territory size should increase with body mass similarly to female home range size, assuming that the resultant degree of polygyny remained independent of body mass. However, the correlation between male territory size and body mass (Fig. 9.4) is much weaker than the correlation between female home range size and body mass (Fig. 6.3) This suggests that either (i) resource gradients are steeper for larger species than for smaller ones, so that it is easier for males of larger species to hold an adequate 'harem' of females within a relatively smaller area; (ii) the effective degree of polygyny decreases with increasing body mass, or (iii) there are other constraints affecting territory size besides bioenergetic demands.

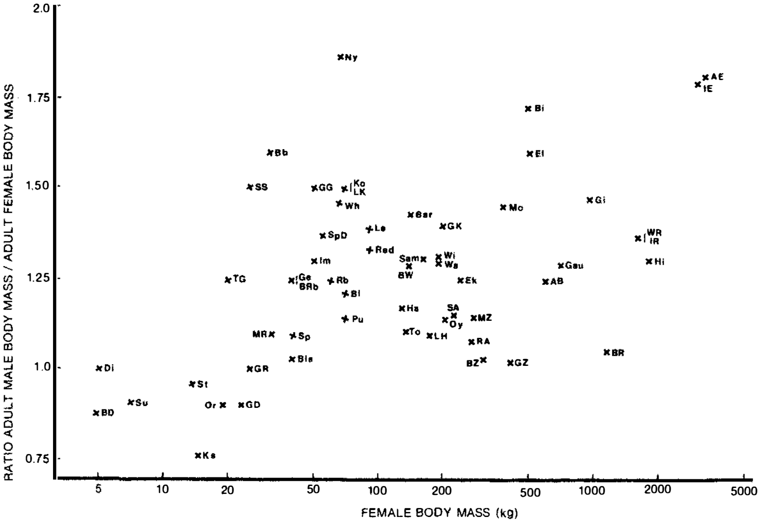

Fig. 9.5 Size dimorphism in adult mass between the two sexes in relation to body mass for various large herbivores. Sources of body mass data are listed in Appendix I.

For ungulates there is an overall positive correlation between the size dimorphism between the sexes and body mass (Fig. 9.5). However, this is due simply to the fact that antelope species under about 25 kg in body mass generally exhibit reverse sexual dimorphism, i.e. females larger than males. If these species are excluded, no significant correlation with body mass remains. Instead tribal or family patterns are apparent. The tragelaphine antelopes are all strongly dimorphic, irrespective of body size. All equids are monomorphic. Among megaherbivores there is a complete range in pattern. Both species of elephant exhibit extreme size dimorphism; white rhino, Indian rhino and hippo are moderately dimorphic; while in black rhino adults of both sexes are of similar size.

There is furthermore no correlation among ungulates between size dimorphism and the degree of polygyny as estimated by PSME (Fig. 9.6). For white rhinos the estimated PSME, based on the mean female population in the most favorable territory in the Madlozi study area, is somewhat on the low side; but it is no lower than that estimated for greater kudu, a strongly dimorphic species. No relation is apparent between estimated PSME and the system of male dominance, whether territorial or other.

The assumed relation between sexual dimorphism and degree of polygyny incorporates the further assumption that male success in combat is directly related to intraspecific variation in body size. However, this need

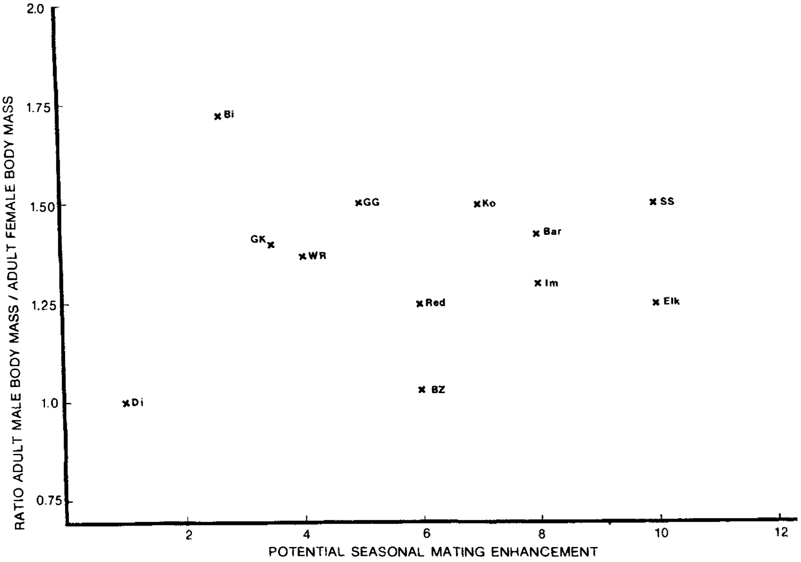

Fig. 9.6 Size dimorphism between the sexes in relation to the Potential Seasonal Mating Enhancement for ungulate males. Data from Clutton-Brock *et al.* (1982); Floody & Arnold (1975); Grubb (1974); Hendrichs & Hendrichs (1971); Klingel (1969); Lott (1979); Murray (1982a); McCullough (1969); Owen-Smith (1984); Schaller (1967); Walther (1972b).

not be the case. Fights amongst zebras and other equids, for example, test agility in both offence and defense, rather than strength (Klingel 1975; Berger 1981). Correspondingly there is a lack of size dimorphism in these species. In species where fights involve bashing or pushing contests, as in sheep (Geist 1971), buffalo (Sinclair 1974), kudu (Owen-Smith 1984), and elephants (Kuhme 1963; Short 1966), mass is clearly a factor. In general, as body size increases, fights tend to be decided more on body mass and strength and less on agility (Geist 1966). This accounts for the common tendency for size dimorphism to increase with increasing body mass.

The fighting technique explanation does not account for the variation in sexual dimorphism among megaherbivore species. In particular both species of African rhino fight in a similar way, using their horns to direct blows into an opponent's body. We thus need to estimate more precisely the effective degree of sexual selection among these species in terms of the potential difference between males and females in their reproductive outputs.

African elephants at Amboseli in Kenya have a mean calving interval of about 5 years, so that on average only 20% of adult females conceive in any

resultant sexual selection factor is close to unity. For sexual selection to be effective in black rhinos, territory sizes would need to be somewhat larger for a given population density, or female distribution would need to be somewhat more patchy. Such requirements seem to be atypical of most black rhino populations.

Thus variations in the degree of size dimorphism among megaherbivores do seem to be related to the degree of sexual selection operating. For size dimorphism to evolve, it is necessary both that male fighting success be dependent on body size, and that males gain sufficient benefit in terms of mating enhancement as a result of the dominance they acquire. This explains the varying patterns found among different groups of animals (Reiss 1986).

Female mate choice

In selecting a mate, females need firstly to recognize conspecific features. Signals used in courtship, whether visual, auditory or olfactory, may serve this basic specific-mate recognition function (Patterson 1985). Nevertheless females may also vary in their responses to different courting males, even though all are of the same species. A female may choose to mate with a particular male (i) because of the superior parental care that he provides, (ii) because of the quality of the resources that he holds, (iii) because of his good genetic constitution, or (iv) because he protects her from the energy-draining attentions of other males (Rubenstein 1980). Females could even favor a particular phenotypic characteristic in a male simply because it has come to serve as a conventional attractant to females, without any other functional value, since sons exhibiting this feature will also be attractive to females (the 'sexy son' hypothesis, Weatherhead 1984).

Among ungulates parental care is not a factor. Superior territory resources are of significance only where the female remains in the male's territory during the critical periods of late pregnancy and lactation. This occurs in some territorial antelope species, for example tsessebe in some regions (Joubert 1972), but is unusual among ungulates. This leaves only hypotheses (iii) and (iv) to be considered.

Males occupying the most favorable territories, or top dominance ranking, may be of superior genetic quality simply in terms of their proven ability to succeed in male–male competition. This may be due to better fighting ability promoted by large size, greater agility, or an edge in physical strength and endurance. Agility and endurance are qualitites that would generally be beneficial to both male and female offspring, for example in terms of ability to evade predators. However, this latter factor is applicable less to megaherbivores than to smaller species. If a male can maintain physical strength despite restricting his foraging to the limited confines of a territory, his food-processing ability is also well tested (cf. the handicap hypothesis, as suggested by Zahavi 1975). In these circumstances, a female simply needs to identify a high-ranking male.

African elephant females actively select older males over 35 years in age as suitors. They attempt to evade courtship advances from younger males, vocalize loudly to attract attention if caught by a younger male, and keep close by an older male if one is present. Moss (1983) suggests that, by favoring older males, females select for factors promoting longevity, which are of benefit to female progeny as well as to male offspring.

Noisy chases are also a feature of courtship in Indian rhinos. Laurie (1982) suggests that these not only test the suitor's strength, but also attract other males, so that the eventual sire is likely to be the strongest male in the area. Hippo copulations are noisy; but where the suitor is the dominant bull in the pool, other bulls do not interfere. In white rhinos, territory boundary blocking interactions between a territory holder and the female he is accompanying are also noisy, but do not attract rival males. A female white rhino gets another suitor only if the male lags so that she is able to elude him and cross into another territory. The premating consort period shown by white rhinos is unusually prolonged, lasting up to 3 weeks. During this time females proceed as if unaware of territory boundaries, so that it is a repeated challenge to the accompanying male to ensure that the female remains within his territory until she becomes receptive to mating. In black rhinos, noisy attacks by the female on the male are sometimes a feature of courtship; but because of the low population densities typical of black rhinos, there is rarely another male nearby.

In all of these cases females gain from the protective influence of a dominant consorting male, so that this proximate benefit cannot be excluded. However, a peculiar feature of the captive breeding of white rhinos helps resolve the issue of female mate choice.

White rhinos initially proved extraordinarily difficult to get to breed in captivity. Some zoos kept male–female pairs of white rhinos for periods exceeding 10 years, without any sexual activity. Females showed no signs of estrus, and males made no courtship advances. From an analysis of the circumstances, Lindemann (1982) concluded that the main requirement for successful breeding was the presence of more than one male. White rhinos produced offspring in 12 out of 28 zoos where more than one male was present, compared with only 3 out of 14 zoos in which two females were present, but only one male. Where just a single male–female pair was kept, there was only one record of breeding. In this exceptional case, the original

techniques dependent upon strength and weight rather than agility, a feature that increases with increasing body mass. However, this potential is expressed only if intrasexual selection among males is effective.

Mechanisms of female choice are a feature of all megaherbivores. These involve either displays to attract other males, tests of the physical prowess of the suitor, or a favoring of the largest and hence oldest class of male. In white rhinos estrous cycling occurs only after a female has experienced a choice of males. Female choice could be due to the potential lag in the gene pool relative to prevailing ecological conditions.

slower breeding rates. However, first order adaptations (or exaptations, in the sense of Gould & Vrba 1982), imposed directly by body size, need to be distinguished from second order adaptations in the form of deviations in life history parameters from those typical of species of a particular size (Western 1979; Millar & Zammuto 1983). Boyce (1979) suggested that, in unpredictable environments, natural selection might favor adaptations enhancing survival through bad times, rather than high rates of population increase.

Several recent reviews have considered relationships between life history variables and body mass. Generally a proportional increase in adult mass is associated with a corresponding proportional change in a particular life history attribute, so that relations are expressed as power functions of the form $Y = a\ M^b$, where M represents body mass. For example, Fenchel (1974) showed that for all animals, including unicellular organisms as well as both heterotherms and homeotherms, the intrinsic rate of population increase ($r_{\max}$) varies in relation to $M^{-0.28}$. For mammals alone, Hennemann (1983) obtained an almost identical estimate for the exponent ($b = -0.26$).

However, rate of population increase is the resultant of several components: age-specific birth rates, age schedule of deaths, and the age structure of the population. In terms of the reproductive attributes of individual females, it is the outcome of age at sexual maturity, intervals between successive offspring, and the number of offspring produced per litter. It is these attributes that are directly subject to natural selection.

Blueweiss *et al.* (1978) found for a wide range of mammals that litter weight varied in relation to $M^{0.82}$, gestation time in relation to $M^{0.26}$, average life span in relation to $M^{0.17}$, and time to sexual maturity in relation to $M^{0.27}$. For African artiodactyls alone, Western (1979) reported that gestation periods varied as a function of $M^{0.16}$, age at first reproduction as $M^{0.27}$, longevity as $M^{0.22}$, and birth weight as $M^{0.72}$. Values for exponents tend to cluster around either 0.75 or 0.25. Lindstedt and Calder (1981) pointed out that no adaptive explanation is required for such power relationships; they follow as inevitable consequences of the allometry of the underlying physiological processes. Time periods for unit metabolic action, such as maturation period, birth intervals and lifespans, tend to be scaled in relation to body mass to the power about one quarter; and volume or mass rates, such as litter mass, in relation to body mass to the power three-quarters.

In this Chapter I focus attention on the life history components determining the reproductive investments of female large herbivores. The

years later also tends to occur during the wet season. Calves born during the dry season also face additional rigors from the daily travelling to and from water.

Hall-Martin, Skinner & Van Dyk (1975) related the wet season conception peak of giraffe to optimal nutritional conditions for the female at the time of estrus, rather than to any influences on the survival of the offspring. They suggested that the extended lactation period reduced the effects of season of birth on calf survival.

In white rhinos the gestation period is 6 months shorter than that of elephants. Thus the birth peak and the conception peak cannot both occur during the same season, as is the case in elephants. For white rhinos the two mating peaks both fall during the wet season, with the resultant birth peaks occurring during the dry season. A similar pattern is shown by both black rhinos and giraffes in southern Africa (Chapter 7). Thus it appears that it is the proximate effect of nutrition on estrous cycling that governs seasonal breeding in megaherbivores, rather than any ultimate consequences of when the calves are born. Hippo follow the early dry season mating – wet season calving pattern typical of smaller ungulates, but their gestation period is only 8 months.

For megaherbivores the critical periods influencing offspring survival, including late pregnancy, early lactation and weaning, are drawn out through different periods of the year, so that there are no strong selective pressures favoring any particular time for reproduction. With no photoperiodic control of estrous cycling, ovarian activity is responsive to the prevailing nutritional regime.

Observations on white rhinos suggest it is the suppressant effect of adverse protein or energy balance on ovarian activity that controls seasonality in reproduction, rather than a stimulatory effect of high nutrition. Failing conception, estrus recurred at intervals of about 30 days. However, females failed to show signs of estrus when the next cycle coincided with a midsummer drought. Some females came into estrus as late as June (mid-dry season) in a year when fresh grass growth occurred in this month. No conceptions occurred during the peak dry season months of August–September. Under equatorial conditions where seasonality in plant growth is less extreme, and may vary between years in relation to the timing of the long and short rains, elephants and black rhinos show no clear seasonal patterns in reproduction. Even in subtropical regions, birth seasons of these species can vary between years in response to rainfall variability. This mechanism explains some of the variability in calving intervals shown by megaherbivore females.

are three clusters: (i) small antelopes, which tend to conceive during or at the end of their first or second years of life; (ii) medium- to large-sized antelopes, which under favorable conditions can conceive as yearlings, but more usually experience their first fertile estrus as two-year-olds; (iii) megaherbivores plus buffalo, which show much individual and population variability in age at first conception. Under zoo conditions, conception may occur as early as 2.4 years among hippos (Dittrich 1976), 3.0 years in Indian rhinos (Lang 1967), and 3.7 years in white rhinos (Lindemann 1982). In the wild, first conception may be delayed as late as 8.2 years in black rhinos (Hitchins & Anderson 1983), 12 years in hippos (Laws 1968a) and 18 years in African elephants (Laws *et al.* 1975). Notably, among megaherbivores the youngest observed ages at first conception are close to those expected on the basis of the overall trend with body size.

For medium-sized antelope, potential longevity is typically about 15–20 years (Western 1979). Eighteen percent of this is about 3 years, which is the usual age at first parturition among these species. Most megaherbivores also produce their first offspring at about 18% of their potential lifespan (Table 10.1). The exceptions are African elephant and hippo, for which reported ages at puberty are commonly longer than predicted by this rule. This discrepancy could be due to the suggested overestimation of ages in this range for these two species (see Chapter 7).

Thus megaherbivores show tendencies towards delayed sexual maturity as expected of *K*-strategists. However, rather than being a species-typical constraint, this retardation of reproduction is apparently a flexible response adjusted to the prevailing ecological circumstances.

Birth intervals

Intervals between births incorporate the gestation period, but need not be directly related to it, since there can also be a variable interval between parturition and the next fertile estrous cycle. The data I will use represent the mean calving intervals of prime-aged females in natural populations. Where a range of values for different populations has been reported, I have chosen the shortest reliably estimated mean value. Where data are available for tropical conditions with breeding largely independent of the seasonal cycle, I have selected these in preference to southern African figures. Beyond this, it is not possible to make allowance for variations in demographic vigor between populations.

For African large herbivores, the birth interval (*BI*) in months is related to adult female body mass according to the relation $BI = 3.4\ M^{0.27}$ (Fig.

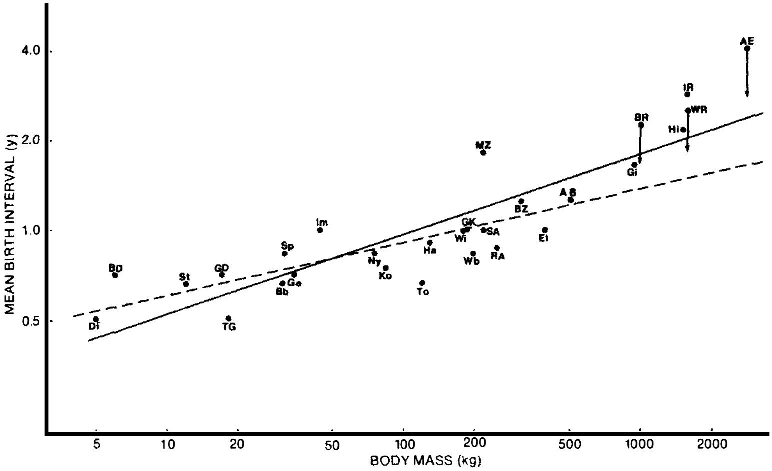

Fig. 10.2 Birth intervals of African large herbivores in relation to body mass. Points represent mean intervals between successive births reported for prime females in natural populations (see text); for white rhino, black rhino and African elephant the shortest reported birth interval is indicated by an arrow. Key to species labels given in Appendix I. Data from Anderson (1978), Bigalke (1970), Buechner *et al.* (1966), Chalmers (1963), Cumming (1975), Duncan (1975), du Plessis (1972), Goddard (1970a). Gosling (1974), Grobler (1980 and personal communication), Hendrichs & Hendrichs (1971), Hillman (1979), Hitchins & Anderson (1983), Huntley (1971), Hvidberg-Hanson (1970), E. Joubert (1974), Laurie (1978), Leuthold & Leuthold (1978), Morris & Hanks (1974), Murray (1980), Roth *et al.* (1972), Simpson (1968, 1974), Sinclair (1977), Skinner & Van Zyl (1969), Smuts (1975c, 1976), Spinage (1970), Von Ketelholdt (1977), Von Richter (1971), Watson (1969), Western (1979), Wilson (1966) and Wilson & Clarke (1962).

Regression lines:

(i) all species (solid): BI(months) = $3.4M^{0.27}$ (SE(b) = 0.029, R^2 = 0.77, N = 28, P = < 0.0001).

(ii) excluding megaherbivores (dashed): BI(months) = $5.0M^{0.17}$ (SE(b) = 0.033, R^2 = 0.56, N = 22, P = < 0.0001).

10.2). For megaherbivores, mean birth intervals all fall above the regression line. However, the shortest individual calving intervals for white rhino, black rhino and African elephant lie close to this regression line. If megaherbivores are excluded, the slope of the regression is somewhat less steep (b = 0.17), and even the minimum values for megaherbivores fall well above the regression line.

Theory suggests that birth intervals, as a time factor, should vary in relation to an exponent of 0.25. It seems that variability in birth intervals among bovids and equids from impala to buffalo size is constrained by the annual cycle. With this consideration, the overall trend including

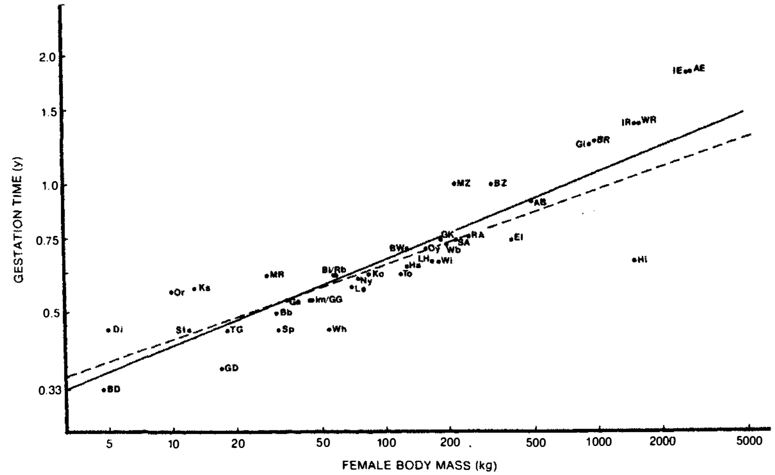

Fig. 10.3 Gestation times of African large herbivores in relation to body mass. Key to species labels given in Appendix I. Data from Dittrich (1972, 1976), Mentis (1972), Smithers (1983), Von Ketelholdt (1977), Western (1979). Regression lines:

(i) all species (solid); $BM(\text{kg}) = 3.15M^{0.20}$ (SE(b) = 0.018, $R^2 = 0.78$, $N = 39$, $P = < 0.0001$).

(ii) excluding megaherbivores (dashed): $BM(\text{kg}) = 3.49M^{0.17}$ (SE(b) = 0.019, $R^2 = 0.73$, $N = 33$, $P = < 0.0001$).

megaherbivores may be taken as more generally valid. Thus the shortest calving intervals recorded for megaherbivores are close to the values expected on the basis of their body size, while the mean birth intervals found in populations tend to be somewhat longer than this. Lengthened birth intervals can be interpreted as an ecological adjustment to food restrictions, which come into effect when populations reach densities close to the environmental carrying capacity *K*.

Gestation times show a closely similar pattern to that exhibited by birth intervals. For all African large herbivores, gestation time scales in relation to an exponent of 0.20; while if megaherbivores are excluded, a slightly lower exponent of 0.17 is obtained (Fig. 10.3). The latter figure is almost identical to the value of 0.16 reported by Western (1979) for artiodactyls alone. However, Martin & MacLarnon (1985) found, using reduced major axis regression, that gestation time for artiodactyls varied in relation to $M^{0.13}$. By considering trends shown by the different grades apparent among mammals, they concluded that the best fit value for the exponent relating gestation time to maternal body mass is 0.10. Megaherbivores apparently show somewhat longer gestation times than expected for their body mass on the basis of the general trend among mammals, with hippo a notable exception. However, the trend in gestation times is somewhat flatter than that expected for a time period parameter. It appears likely that variability in gestation times among medium-sized mammals has been constrained by the need to synchronize reproduction with the seasonal cycle.

In African elephants, fetal growth does not get under way until 20% of gestation time has passed; while among other mammals, this initial lag is generally assumed to occupy no more than 10% of gestation (Craig 1984). If this difference is general among megaherbivores, it could account for most of the extra gestation time shown by these very large species.

Among African ruminants, the relation between mean birth interval and potential longevity is such that the potential lifetime reproductive output of a female is about 14 offspring (Georgiadis 1985). Megaherbivores, except for African elephant, conform to this pattern (Table 10.1). This is a further indication that ages have commonly been underestimated in this species (Chapter 7). An elephant female attaining puberty at 10 years and calving every 3.8 years would produce 13 offspring during a 60 year lifespan, which conforms more closely with the data for other species.

Maternal investment in reproduction

Reiss (1985) suggested that the maternal energy available for reproduction is equal to the difference between the energy assimilation rate and the energy required for maintenance. Both of these factors are scaled allometrically, with estimates for the power coefficient b varying between 0.52 and 0.95. Hence, maternal reproductive investments must also be scaled in relation to body size with the exponent b falling within this range.

However, as was shown in Chapter 3, food intake by females may vary in relation to stage of pregnancy or lactation. Generally the maternal contribution to the young peaks shortly after birth, but before the young secure significant amounts of food from the environment. Millar (1977) derived a formula expressing the peak reproductive effort in terms of the relation between the metabolic demands of the young at commencement of weaning, and the maintenance metabolic demands of the mother, i.e. $n \times m^{0.75}/M^{0.75}$ (where n = litter size, m = mass of individual young at weaning, and M = maternal body mass). For a wide range of mainly small mammals, he found that birth mass scaled in relation to $M^{0.71}$, weaning mass in relation to $M^{0.73}$, and reproductive effort (according to the above formula) in relation to $M^{-0.17}$. Thus larger mammals invest less in reproduction, relative to their maintenance metabolic requirements than smaller mammals.

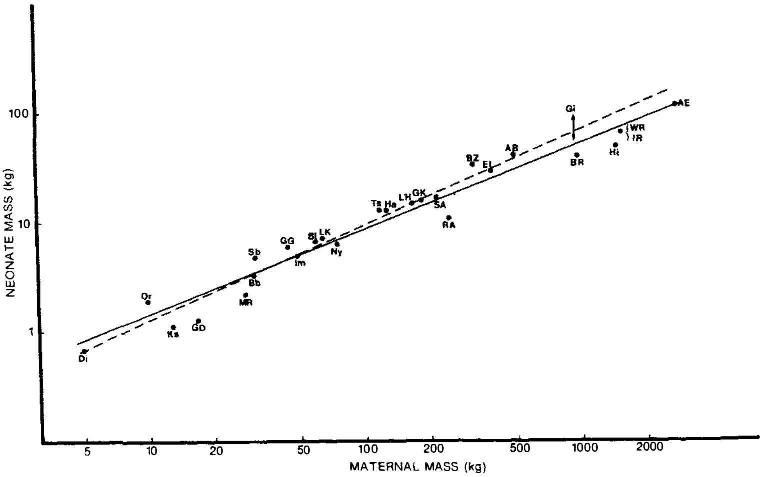

Fig. 10.4 Neonate mass in relation to maternal mass for mainly African large herbivores. Points represent mass at birth for each species, including both zoo and field data (except for giraffe where upper arrow indicates data from wild, lower arrow data from zoos). Key to species in Appendix I. Data from Ansell (1963), Dittrich (1972), Hall-Martin & Skinner (1978), Lang (1961), and references given for Fig. 10.2.
Regression lines:
(i) all species (solid): $BM(\text{kg}) = 0.23M^{0.79}$ (SE(b) $= 0.031$, $R^2 = 0.96$, $N = 27$, $P = < 0.0001$).
(ii) excluding megaherbivores (dashed): $BM(\text{kg}) = 0.17M^{0.87}$ (SE(b) $=$ 0.044, $R^2 = 0.95$, $N = 21$, $P = < 0.0001$).

Data on neonate mass are most readily available for zoo-kept animals. I have simply averaged the published records for a species without regard to their source (whether zoo or wild animals) or the sex of the offspring (males generally weigh more than females at birth).

For large herbivores, neonate mass increases as a function of maternal mass to the power 0.79 (Fig. 10.4). This is identical to the value for *b* reported for various ungulates by Robbins & Robbins (1979). For both white rhinos and African elephants, the weight of the newborn young represents about 4% of the mother's weight, compared with 9% for medium-sized antelope such as kudu, and 13.5% for the smallest antelope, dikdik. In this case the points for rhinos and hippos, but not for African elephants, fall below the regression line. If megaherbivores are excluded, a higher estimate for *b* of 0.87 is obtained. This is greater than the power coefficient for birth weight of 0.72 found by Western (1979); but almost identical to that reported by Martin & MacLarnon (1985) for artiodactyls. Thus megaherbivores produce somewhat smaller offspring than expected from the trend among other African ungulates. This could simply be a consequence of the tendency for gestation periods to increase less steeply with increasing body mass than expected for a time period parameter.

Martin & MacLarnon (1985) refine the analysis further by taking into account grade differences between precocial and altricial species. They found neonatal mass to be related to $M^{0.91}$ for mammals with precocial young in general; while for artiodactyls alone neonatal mass is related to $M^{0.89}$. However, the overall best fit value for the exponent relating neonate mass to maternal mass is 0.80. This agrees closely with the value of 0.79 that I obtained for all large herbivores in Fig. 10.4. Thus in terms of offspring mass, females of larger species appear to invest slightly more in reproduction, relative to their maintenance metabolic requirements, than smaller mammals; although somewhat less as a fraction of maternal body mass.

Maternal investments can be estimated alternatively in terms of the milk energy supplied to the young at peak lactation. This has been found to scale in direct relation to the maintenance metabolic rate of the mother, i.e. $M^{0.75}$. Thus the peak lactational energy output of female mammals tends to be a constant fraction of their maintenance metabolism. Furthermore, the metabolic demands of sucking young are proportional to their mass to the power of 0.83, rather than 0.75. The total metabolic mass of the litter proves to be a more reliable predictor of milk energy yield than maternal metabolic mass (Oftedal 1984).

Oftedal (1984) suggested that the ratio between the metabolic demands of the young (proportional to $M^{0.83}$), and the maintenance metabolism of the mother (proportional to $M^{0.75}$), was the most widely applicable index of maternal reproductive effort. Among the eight ungulate species producing single young for which data were presented, values for this ratio vary from 0.55 for goats to 0.34 for beef cattle and red deer and 0.28 for reindeer. Megaherbivores show considerably lower values for this ratio (Table 10.2). This implies that females of these very large species make lower peak investments in reproduction, relative to their maintenance metabolic requirements, than do smaller ungulates.

However, the overall lifetime investment by females in reproduction extends over the whole period of each reproduction cycle, including any interim when females are neither pregnant nor lactating. Additional metabolic costs are incurred in transforming maternal energy into offspring biomass or milk. Insufficient data are available to attempt a comparative analysis in terms of lifetime reproductive investments for a range of large herbivore species. Thus I will merely illustrate such calculations for the two ungulate species with which I am personally familiar from my own field research: the white rhino, as a representative megaherbivore; and the greater kudu, as a representative ungulate of medium–large size.

Table 10.2. *Ratio between the metabolic mass of the offspring and maternal metabolic mass for megaherbivores*

Species	Maternal mass (kg)	Neonate mass (kg)	Metabolic mass ratio[a]	
			Birth	Weaning
African elephant	2800	120	0.138	—
White rhinoceros	1600	65	0.126	0.196
Indian rhinoceros	1600	65	0.126	—
Black rhinoceros	1000	40	0.120	—
Hippopotamus	1400	50	0.112	—
Giraffe	850	55[b]–93[c]	0.177–0.273	—

Notes: [a] $m^{0.83}/M^{0.75}$, where m = offspring mass, M = maternal mass.
[b] zoo data. [c] wild data.

The maternal investment in reproduction can be partitioned between the periods of pregnancy and lactation. Within each of these it can be separated into two components: (i) the maintenance metabolic costs of the offspring, proportional to offspring mass to the power three-quarters; (ii) the growth increment of the young, related to the energy content of this mass. The latter is assumed to be about 25kJ per gram of biomass, while the former is equal to 293 times $M^{0.75}$ kJ on a daily basis. To simplify calculations I will ignore variations in the utilization of metabolizable energy, as well as activity increments. However, the efficiency of utilization of energy for milk production is only about two-thirds of that for maternal growth, and this must be taken into account (Moen 1973).

Since inadequate data are available to integrate the maternal contribution on a daily basis, calculations will be simplified by summing the mean maternal investments over set periods. During the first two-thirds of pregnancy, the energy requirements of the fetus will be assumed to be negligible. During the penultimate sixth of pregnancy, its mean mass will be taken as one fifth of the birth mass; and during the final sixth, as one half of birth mass. These masses will be used to calculate the daily maintenance requirements of the fetus, which are then multiplied by the duration in days of each period. The investment in neonatal growth will be based on the birth mass. The period of infancy leading up to weaning will be divided into four periods, corresponding to those for which estimates of grazing time relative to that of the mother were made (Table 8.2). It will be assumed that the relative grazing time reflects the proportion of its energy requirements that the calf gets from the vegetation, with the mother's milk contribution making up the remainder. Finally, the energy contribution of the mother to the offspring needs to be related to her own basal metabolic requirement.

The latter is equal to 293 $M^{0.75}$ kJ per day, summed over the whole period between successvie births. Based on a calving interval of 30 months, the relative proportion of her own maintenance requirements that a white rhino mother devotes to reproduction is estimated to be 22.7%. For the minimum observed calving interval of 22 months, this proportion increases to 31%.

Adult female kudus attain a body mass of 180 kg. The birth mass of a kudu offspring is 16 kg, the period to the end of weaning is 6 months, and the weight of the offspring at the end of this period is about 60 kg. No data are available on the proportion of its energy requirements that the young secures from the vegetation. These will be assumed to be the same as those recorded for white rhino calves for corresponding segments of the period to weaning. Calculations suggest that an annually breeding kudu female invests 33% of her maintenance energy requirements in reproduction.

Hence it seems that a white rhino female breeding at the shortest observed interval makes the same reproductive effort as a typical large antelope female. However, white rhino females generally do make a lower reproductive investment than is typical of medium-sized ungulates, due to the fact that their calving intervals tend to be about one-third longer than the minimum. On the other hand, the reproductive investment of the typical antelope female is also reduced by perhaps one-third by the fact that on average about 50% of calves die shortly after birth (personal observations); while for white rhinos infant mortality is negligible.

Hence it is evident that, in order to calculate the effective reproductive investments by ungulate females, a number of factors have to be taken into account. These include not only the peak reproductive effort made after offspring are produced, but also the intervals between reproductive episodes, and the likelihood of the young surviving. Typical lifetime investments in reproduction made by female megaherbivores appear to be no different from those shown by medium-sized ungulates. Megaherbivores show great flexibility in birth intervals, in relation to ecological circumstances; if conditions are unfavorable, either conception is delayed, or the fetus is aborted early in pregnancy. The lag in commencement of fetal growth found in African elephants could allow a period for abortion with minimal costs to the mother. Small and medium-sized ungulates generally produce offspring according to schedule, unless conditions are exceptionally unfavorable. Neonatal mortality adjusts birth rates to the prevailing circumstances. The reproductive costs of unsuccessful attempts are minimal where breeding is coupled to the seasonal cycle; a delay in conception would simply result in the young being born at an unfavorable time of the year, and so unlikely to survive anyway.

in the cycle (Verme & Ozaga 1981); (ii) male fetuses show a higher *in utero* mortality than do female fetuses (Robinette *et al.* 1957). The latter pattern could simply be an effect of the more rapid growth rate, and hence higher nutritional demands, of males relative to females, so that male offspring are more vulnerable under conditions of food deprivation (Clutton-Brock, Albon & Guinness 1985).

In all of the larger ungulates, male reproductive output is influenced by dominance status and thus tends to be more variable than that of females. Furthermore, in most species male reproductive performance is dependent on body size. Thus the potential exists for facultative variations in natal sex ratio, although the mean sex ratio should not deviate far from 1 : 1.

There is no reason to expect the pattern among megaherbivores to differ from that shown by medium-sized ungulates. Nevertheless, available data on the perinatal (fetal or birth) sex ratio reveal a tendency for the proportion of male offspring to increase with increasing body size (Fig. 10.5). This tendency is statistically significant if the data point for the single small antelope species in the sample, steenbok, in excluded. Steenbok show a more extreme sex ratio bias in favour of males (2 : 1) than has been recorded for any ungulate, based mostly on a single sample. Notably, steenbok also show reverse sexual dimorphism, i.e. females larger than males. Apart from steenbok, the next highest sex ratio is that shown by white rhino (combining all samples). Other species showing a perinatal sex ratio exceeding 120 males : 100 females include two other megaherbivores (black rhino and giraffe) and one large cervid (moose). African elephant and hippo show fetal sex ratios close to parity.

In both rhino species, females disperse from the maternal home range; and neither in moose nor in giraffe are there persistent associations between mothers and daughters. In contrast, young elephant and hippo females remain associated with their mothers. Hence these extremely male-biased sex ratios cannot be explained in terms of the post-weaning costs of female progeny.

In the case of white rhino, young females produced a higher proportion of male calves, and also exhibited shorter birth intervals, than old females (Table 8.9). The predominance of male offspring born at Umfolozi during the study period can be ascribed in part to the high proportion of young females in the expanding population. Over this period the population was increasing at a higher rate than had been shown earlier. Thus it appears that habitat conditions were favorable for white rhinos, despite below-average rainfall. Since no sex ratio bias was evident among the adult and subadult segments at the time of my study, the sex ratio bias among calves born

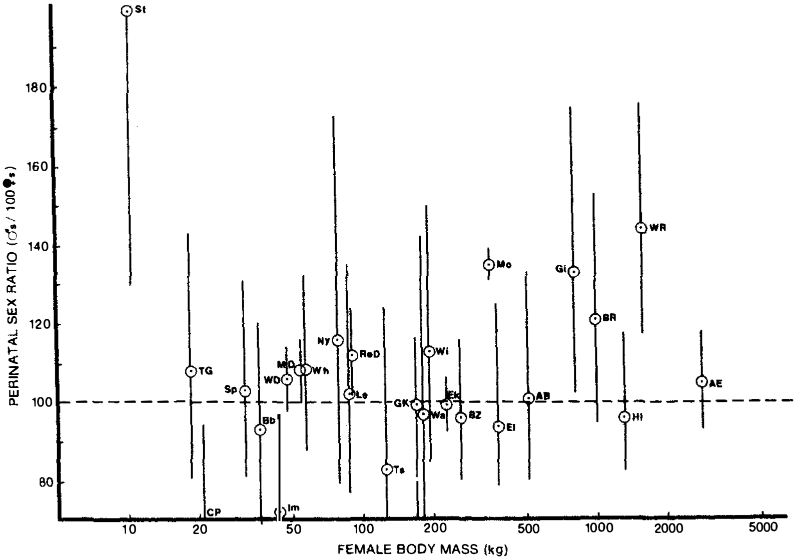

Fig. 10.5 Perinatal sex ratios of various large herbivores in relation to body mass, based on sex ratios recorded for either fetuses or new born calves, combining data from all sources, zoo records as well as wild populations. Lines indicate 95% binomial confidence limits; dashed line indicates even sex ratio. Key to species labels given in Appendix I. Data from Attwell & Hanks (1980), Allen-Rowlandson (1980), Child *et al.* (1968), Clough (1969), Clutton-Brock *et al.* (1982), Frame (1980), Goddard (1970a), Hall-Martin (1975), Hanks (1972b), Hitchins & Anderson (1983), Houston (1982), Huntley (1971), Hvidberg-Hansen (1970), Klingel (1965), Klös & Frese (1981), Laurie (1978), Laws (1969a), Laws & Clough (1966), Leuthold & Leuthold (1978), Lindemann (1982), Mason (1982), Mentis (1972), Mitchell *et al.* (1977), Morris & Hanks (1974), Mossman & Mossman (1962), Pienaar *et al.* (1966a), Reuterwall (1981), Robinette & Archer (1971), Robinette & Child (1964), Roth *et al.* (1972), Sherry (1975), Simpson (1968), Sinclair (1977), Smuts (1974, 1975c), Smuts & Whyte (1981), Sowls (1974), Spinage (1982), Talbot & Talbot (1963a), van Zyl & Skinner (1970), Verme (1983), Watson (1969), Williamson (1976), Wilson & Child (1964, 1965), Wilson & Clarke (1962), Wilson & Kerr (1969).

during the study period must have been a new phenomenon (see Chapter 12). The sex ratio bias towards males among zoo-kept white rhinos can likewise be ascribed to a predominance of young females, since young animals are preferentially acquired and no zoo has held white rhinos for very long.

Among mule deer, primaparous females showed a fetal sex ratio of 122 males : 100 females, compared with 106 males : 100 females for older mothers (Robinette *et al.* 1957). However, red deer showed no difference in natal sex ratio between first-time mothers and older females (Clutton-Brock, Guinness & Albon 1982). Instead dominant hinds produced a higher proportion of sons than did subordinate hinds (Clutton-Brock, Albon & Guinness 1984). The latter pattern suggests that good female body condition may have a positive influence on the proportion of sons. In contrast, among white tailed deer and mule deer females on a poor plane of nutrition produce a higher proportion of male progeny (Verme 1983). A feature of these small deer is that they commonly produce multiple offspring, with the sex ratio of litters of one significantly more male-biased than litters of two or three. The fact that these deer produce more daughters than sons when in good condition could be explained on the grounds that it is more advantageous for mothers to produce a large litter than a large son in such circumstances. Scandinavian moose, for which the birth sex ratio averages 135 males: 100 females ($N = 160\ 911$), show a high frequency of twinning (Reuterwall 1981).

None of the above hypotheses explains the bias in birth sex ratio towards males shown by black rhinos or giraffes. The fact that certain megaherbivores produce more extremely male-biased sex ratios than is typical of smaller ungulates could simply be a consequence of their variable birth intervals. The flexibility in time to conception provides scope for selective abortion of embryos of the less advantageous sex, with less effect on reproductive output than is the case for smaller species with restricted breeding seasons.

Summary

The fundamental features distinguishing megaherbivores from smaller ungulates are these:

1. Prolonged and highly variable times to puberty are typical of both males and females, with these times sensitive to prevailing nutritional conditions. Among males social maturity is delayed several years after puberty.
2. Gestation periods exceed one year, so that birth intervals usually span two years or longer. With sensitive periods of reproduction spread out over the seasonal cycle, there is no strong selection for a restricted breeding season. Female sexual cycling thus responds directly to the prevailing nutritional conditions.
3. Peak maternal investments in lactation are lower than those of smaller ungulates. However overall lifetime investments in reproduction appear no different from those of medium-sized bovids. Megaherbivores show a flexibility in time to conception following

parturition; while smaller ungulates show variability in perinatal mortality, in relation to the prevailing ecological conditions.

4. Due to the flexible birth interval and weak seasonality, the scope for variation in offspring sex ratio, in relation to factors such as age of mother and prevailing habitat conditions, is greater than it is among smaller species.

11

Demography

Introduction

In this chapter I cover those ecological attributes that are features of populations rather than of individual animals. Population ecology is generally framed in terms of the logistic model of population growth. The parameters of this model include (i) the maximum or 'intrinsic' rate of population growth shown when population density is very low, labelled r_{max}; (ii) the equilibrium density or 'carrying capacity' eventually attained, labelled K.

However, rate of population growth is the difference between recruitment, determined by processes of birth and immigration, and losses, the outcome of deaths and emigration. Since natality and mortality rates vary with age and sex, the realized rate of population increase is influenced by population structure. Strictly, r_{max} and K are defined only for populations that have attained an equilibrium age and sex composition. However, real populations seldom remain at any equilibrium for long, due to environmental fluctuations. Furthermore, density varies spatially over the population range in relation to habitat suitability.

The ecological features to be considered in this chapter include (i) population composition, in terms of age structure and sex ratio; (ii) rates of population change with time; (iii) population densities attained.

Population structure

In considering age structure, the functional age classes include (i) adults, i.e. animals that have passed the age of socio-sexual maturity and are reproductively active, or at least potentially so; (ii) juveniles, i.e. animals that have not attained the age of independence from their mothers; (iii) subadults, i.e. animals that are intermediate between the above two categories. Puberty or physiological sexual potency is attained during the subadult

Table 11.1. *Age structure of African elephant populations*

					Age-class proportions (%)					
Area	Time	Segment	Status	Ageing technique	Juvenile (0–5y)	Immature (5–10y)	Subadult (10–15y)	Young adult (15–20y)	Adult (20+y)	Reference
Manyara, Tanzania	1970	All	Increasing	Height	29	19	14	5	33	Douglas-Hamilton 1972
Hwange, Zimbabwe	1971–72	Females	Increasing	Dentition	26.5	15	16.5	6	36	Williamson 1976
Kruger, South Africa	1968–74	Females	Increasing	Dentition	29.5	16.5	19.5	5.5	29	Smuts 1975c
Kasungu, Malawi	1978	All	Increasing	Height	35	24.5	8.5	7.5	24.5	Jachmann 1980
Luangwa, Zambia	1968–69	Females	Stable?	Dentition	18.5	13.5	12	8	48	Hanks 1972
Tsavo East, Kenya	1962–66	All	Stable?	Length	31	20	11	8	29.5	Leuthold 1976a
Tsavo East, Kenya	1974	All	Recovering	Length	11.5	19.5	17	10.5	41.5	Leuthold 1976a
Tsavo West, Kenya	1974	All	Recovering	Length	23.5	21	11	8.5	36.5	Leuthold 1976a
Murchison Falls south, Uganda	1966	All	Declining	Dentition	13	12	12.5	11	51.5	Laws *et al.* 1975
Mean, all populations					24.2	18.0	13.6	7.8	36.4	

adult male segment of the population (Croze 1972; Hall-Martin 1984; Hanks 1972; Laws, Parker & Johnstone 1975; Leuthold 1976b; Moss 1983; Smuts 1975c).

The life tables presented for the Murchison Falls, Uganda, population indicate an adult sex ratio of 73 males : 100 females. At Tsavo in Kenya, the population sex ratio was 80 males : 100 females. In the Kruger Park in South Africa, the sex ratio of animals up to 14 years (i.e. prior to the age at which males leave family groups) was 98 males : 100 females, while the sex ratio for the total population was estimated to be 95 males : 100 females. Since adults (> 15 years by Laws' method) made up 35% of the Kruger Park population, an adult sex ratio of 92 males : 100 females is indicated. This is based on the period 1968–74. In 1964 an adult sex ratio of 107 males : 100 females was recorded, suggesting a greater preponderance of bulls among the elephants initially colonizing this park. In the Kasungu Park in Malawi, the adult sex ratio was 55 males : 100 females, due largely to selective shooting of males in crop protection and by poachers (Laws 1969a, 1969b; Jachmann 1986; Pienaar, van Wyk & Fairall 1966b; Smuts 1975c).

Only limited data are available for Asian elephants. The proportion of adults in the Ruhunu Park in Sri Lanka was 65%. The adult sex ratio of the combined population sample from various parks in Sri Lanka is 35 males : 100 females, a difference related to greater dispersal and mortality among subadult males (McKay 1973; Santiapillai, Chambers & Ishwaran 1984).

Hippopotamus

Among 932 female hippos culled in Uganda and the adjoining lakeshore region of Zaire, 72.5% were sexually mature, 9% pubertal and 18.5% immature. In a sample of 585 hippos of both sexes shot in the Luangwa River in Zambia, 78% were aged over 10 years. Of 225 hippos culled in the Kruger Park in South Africa in 1974–75, 68% were adult (> 10 years). The Kruger Park population was believed to be increasing following earlier drought losses, while other populations were probably stable. However, young hippos are difficult to shoot and retrieve from the water, so that all samples overestimate the proportion of adults.

In the Uganda sample, the adult sex ratio was 72 males : 100 females ($N = 1421$) for animals culled along lakeshores, but 196 males : 100 females ($N = 740$) among animals culled in ponds away from the lake. At Luangwa, the adult sex ratio was 89 males : 100 females ($N = 312$) for animals shot during the first year of culling; but 63 males : 100 females ($N = 145$) among animals culled from the same section of river the following year, when less effort was expended on small groups in isolated pools. In the Kruger Park, animals culled from various rivers over 1974–77 showed a sex ratio of 52 males : 100 females ($N=463$) among all age classes. The sex ratio of adults > 10 years was 41 males : 100 females ($N=154$). Since males do not achieve full growth, and hence dominant breeding status, until at least 26 years old, the functional sex ratio was 25 males : 100 females ($N=109$). However, the strongly female-based sex ratio in the Kruger Park sample was probably due in part to dispersal by a proportion of males into isolated pools and dams away from the rivers where shooting was carried out. Hippos shot in Kruger Park in 1964 under drought conditions, when animals were crowded in remaining river pools, showed an even sex ratio (Laws & Clough 1966; Pienaar, van Wyk & Fairall 1966; Marshall & Sayer 1976; Smuts & Whyte 1981).

Giraffe

The increasing giraffe population in the Serengeti Park in Tanzania contained 52% adults (> 5 years), while the Nairobi Park population in Kenya contained 56% adults. The adult sex ratio at Serengeti was 70 males : 100 females; at Nairobi Park it was 80 males : 100 females; while at Timbavati in South Africa it was 75 males : 100 females. Since the birth sex ratio is biased in favor of males, this indicates considerably higher mortality or dispersal by males relative to females (Foster & Dagg 1972; Hall-Martin 1975; Pellew 1983a).

Rhinoceroses

The Indian rhino population at Chitwan in Nepal contained 52% adults, 21% subadults and 26.5% juveniles. The sex ratio of adults was 62 males : 100 females. These proportions are based on functional age classes, i.e. females were classed as adult once they had given birth, while males were not classed as adult until fully grown at about 10 years (Laurie 1978).

Healthy black rhino populations in various parts of East Africa contain about 60% adults (fully grown, i.e. older than about 8 years), compared with 82% adults in the declining Hluhluwe Reserve population (Table 11.2). Adult sex ratios generally show an excess of males, except for the Tsavo and Serengeti populations.

White rhinoceros

The composition of the white rhino population in the Umfolozi–Hluhluwe complex, and its regional distribution during both wet and dry seasons, was determined from aerial surveys carried out in August 1970 and

Table 11.2. *Age and sex composition of black rhino populations*

Area	*N*	Adults %	Subadults %	Juveniles %	Adult sex ratio (♂s : 100 ♀s)	*N*	Reference
Ngorongoro, Tanzania	108	61	19	20	128	66	Goddard 1967
Olduvai, Tanzania	74	56	24	20	116	41	Goddard 1967
Serengeti, Tanzania	67	66	6	28	83	44	Frame 1980
Tsavo East, Kenya	531	64	13	23	98	338	Goddard 1970a
Amboseli, Kenya	72	61	—	—	126	44	Western & Sindiyo 1972
Hluhluwe, South Africa	199	82	15	3	110	163	Hitchins & Anderson 1983
Umfolozi–Corridor, South Africa	129	72.5	15.5	12	125	94	Hitchins & Anderson 1983

Table 11.5 *White rhino population structure from ground samples outside the study areas*

Area	Period	*N*	Ad♂ (%)	Ad♀ (%)	Subadult (%)	Calf (%)
1. Western section of Umfolozi Game Reserve:						
(a) Madlozi environs	Aug–Sept 1969	138	16.0	22.5	43.5	18.1
(b) Nqolothi–Mfulumkhulu	Oct 1969	24	—	—	—	—
(c) Nqutsheni environs	Jan 1969	45	13.3	31.1	26.7	28.9
(d) Gqoyini environs	Mar 1969	18	—	—	—	—
Combined, Umfolozi West		225	16.0	25.8	37.3	20.9
2. South of W. Umfolozi River:						
	Feb 1971	61	27.8	28.5	21.3	21.3

Table 11.6. *Estimated overall composition of the white rhino population in the Umfolozi–Corridor–Hluhluwe complex, as of early 1969*

Upper figure is estimated percent from population samples.
Lower figure is calculated total number of rhinos.

Region	Population size	Ad♂	Ad♀	Subad.	Calf
1. Umfolozi Game Reserve:					
(a) West		18	27	32	23
	1100	198	297	352	253
(b) East		16.5	23	40	20
	177	30	41	72	35
(c) South		27.5	24	27.5	21
	259	71	63	71	54
2. Corridor		25.5	25.5	27	22
	303	77	77	82	67
3. Hluhluwe Game Reserve:					
(a) South		25.5	25.5	27	22
	42	11	11	12	9
(b) North		16	7	70	7
	37	6	3	26	3
Grand total	1918	393	492	615	421
percent		20.5	25.6	32.1	21.9

$N = 461$) applies to the whole population. The reconstructed 1969 population in the whole complex contains 20.5% adult males, 25.6% adult females, 32.1% subadults and 21.9% calves (Table 11.6). However the subpopulation in the western section of Umfolozi, including nearly 60% of the total, included only 18% adult males, with 27% adult females, 32% subadults and 23% calves. In other regions, adult males equalled or outnumbered adult females.

Prior to early 1969 most rhino removals had taken place from outside the boundaries of the Umfolozi Game Reserve. Thus the composition of the reconstructed 1969 population can be regarded as unaffected directly by the capture operations, though influenced by the age structure of those animals dispersing out of the game reserve.

The adult sex ratio in the reconstructed 1969 population is 80 males : 100 females ($N = 684$, based on the total population sample recorded in the two aerial surveys). The adult sex ratio observed in the western study areas was 72 males : 100 females (Table 11.4); while in the population sample from surrounding areas it was 62 males : 100 females ($N = 94$, Table 11.5). This is the functional sex ratio of socially mature males (aged 10–12 years and over) to reproductively active females (aged about 7 years or more).

Table 11.7. *Sex ratio of immature age classes of white rhinos*
Based on number of different individuals recorded in various population samples.

Area	Calves (1–3 yrs)			Subadults Class I (3–6 yrs)			Subadults Class II (6–9 yrs)		
	N	♂	♀	*N*	♂	♀	*N*	♂	♀
Madlozi, Jan 1969	31	15	16	32	16	16	18	11	7
Nqutsheni, 1969	30	11	19	21	9	12	23	20	3
Gqoyini, 1969	18	10	8	28	14	14	5	4	1
Dengezi, 1969	15	10	5	14	7	7	6	2	4
UGR west environs, 1969	19	9	10	13	8	5	9	6	3
UGR south, 1971	3	2	1	8	3	5	4	4	0
Combined	116	57	59	116	57	59	65	47	18
Ratio ♂:♀		97:100			97:100			261:100	

The observed sex ratio among calves and subadults under 6 years was 97 males: 100 females (Table 11.7). Among older subadults there was a preponderance of males, due to the delayed sexual maturity of males relative to females. Taking into account the observed proportions of subadults in the population, the sex ratio of all animals over 6 years of age is calculated to be 98.5 males: 100 females.

Population samples recorded subsequent to my study showed that a male-biased sex ratio had spread into older age classes. A horseback survey during 1974 yielded a sex ratio for adults plus subadults (> 4 years) of 154 males: 100 females (Brooks 1974).

Summary

The proportion of reproductively mature adults is typically about 60–70% in stable populations of megaherbivores, compared with 45–55% in increasing populations. African elephant populations seem to contain a somewhat higher proportion of immatures, and hippo populations a higher proportion of adults, than other species. However, this variability could be due partly to varying interpretations of the ages at which males and females attain reproductive maturity.

The adult sex ratio tends to be even in elephants and white rhinos, except where modified by differential dispersal or shooting. Black rhino populations commonly show an excess of adult males; while in giraffe and hippo the adult sex ratio tend to be female-biased. However, in both hippo and white rhino some males disperse into less suitable habitats, leaving a female-biased sex ratio among the adults remaining in favored localities.

population was augmented by immigration from Mozambique prior to the completion of a border fence in 1974. The number of elephants removed over the period 1974–84 indicates a population growth rate of 7.5% per annum, but some immigration from Mozambique may have continued despite the fence.

The proportion of calves less than one year old in the Kruger Park population averaged 7.0% over a ten year period, indicating the approximate upper bound to the rate of increase in the absence of immigration. The proportion of sub-yearling calves recorded in other elephant populations varies between 6% and 8.5% based on long term averages. However, population samples from single years may show calf proportions varying between 2.4% and 10.4%, due to the effects of varying rainfall on short term fertility (Barnes 1983; Croze 1972; Douglas-Hamilton 1972; Eltringham 1977; Hall-Martin 1980, 1984, unpublished reports; Hanks 1972; Laws, Parker & Johnstone 1975; Lewis 1984; Sherry 1975).

A computer simulation by Hanks & McIntosh (1973) suggested a maximum sustained rate of increase by African elephants of about 4% per annum. This is based on a 3.5 year birth interval, 5% per annum juvenile mortality, 1% per annum mortality of prime adults, and puberty at 12 years. However, if females first conceived at 8 years (as recent evidence suggests), and the mortality of prime adults was only 0.5% per annum, a maximum population growth rate of slightly over 6% per annum could be sustained, based on my own simulation modelling.

The colonization history of the Kruger Park reveals the importance of dispersal as a population process. In 1905 the total population was estimated to be only 10 elephants, restricted to the extreme north. By 1959 the estimated elephant total was still under 1000. At about this time the first breeding herds appeared in the southern section of the park. The first helicopter census carried out in 1964 revealed 2374 elephants, with only 61 elephants, mostly males, in the southern district. In 1967, 6586 elephants were counted and culling commenced. By 1983 the population in the southern district numbered over 1200, including breeding herds as well as males. Most of the population increase was due to immigration from neighboring Mozambique (Hall-Martin 1984).

Park populations of elephants in other parts of Africa, e.g. Murchison Falls in Uganda and Tsavo in Kenya, have also been augmented by immigration, due largely to human settlement and hunting in adjoining regions. Elephants first appeared in the Serengeti Park in Tanzania in 1957, and increased to over 2000 by 1965 (Lamprey *et al.* 1967; Laws 1969b; Laws, Parker & Johnstone 1975).

Among Asian elephant populations, juveniles less than a year old formed 6.5% of the combined sample recorded in the Gal Oya, Lahagula and Yala Parks in Sri Lanka. Thus their potential rate of population increase appears closely similar to that shown by African elephant (McKay 1973).

Hippopotamus

The hippo density per kilometer of river in the North Luangwa Park in Zambia increased from 3.8 in 1950 to 22 in 1972, while that in the South Luangwa Park increased from 5 to 11 over the same period. These population changes suggest annual growth rates of 11% and 6% per annum respectively. In the Queen Elizabeth Park in Uganda, the proportion of calves less than a year old was 6% in 1958 when the population density was very high, but increased to 14% in 1966 following large-scale population reduction. Thus it appears that the potential rate of population increase of hippos exceeds 10% per annum.

At Luangwa an attempt was made to eliminate all hippos from a 24 km section of river. A total of 652 hippos was shot, but 200 hippos moved in to recolonize this section during the following rainy season. The majority of the dispersing animals were adult females (Laws 1968b; Marshall & Sayer 1976).

Giraffe

The giraffe population in the Serengeti Park in Tanzania maintained a growth rate of 6% per annum over the five year period 1971–76. Juveniles less than one year of age formed 15.5% of this population, compared with 11% in the Nairobi Park population. In the Kruger Park population the proportion of juveniles under a year old recorded in dry season surveys was 5.2% when the population was declining, but 7.1% the following year when a population increase was recorded (Mason 1984, 1985b; Pellew 1983a).

Rhinoceroses

The Indian rhino population at Chitwan was estimated to be increasing at a rate of perhaps 6% per annum, based on the population structure, calving rate and estimated mortality (Laurie 1978).

For the black rhino populations at Ngorongoro and Olduvai in Tanzania, recruitment based on calf proportions was estimated to be 7% per annum over the period 1962–66. At Tsavo in Kenya, subyearling calves formed 9.0% of the population; while at Masai Mara this proportion was 7%. Black rhinos introduced into the Kruger Park have maintained a steady rate of increase of 9% per annum.

East African black rhinos are reportedly slow to disperse into new areas. However, the Corridor and Umfolozi Game Reserve have been steadily colonized by black rhinos dispersing from the adjoining Hluhluwe Reserve (Goddard 1967, 1970a; Hall-Martin 1986; Mukinya 1973; Hitchins & Anderson 1983).

White rhinoceros

Censuses of the white rhino population in the Umfolozi–Hluhluwe complex were conducted annually or every other year by the Natal Parks Board from 1959 onwards. Initially these were carried out by fixed-wing aircraft, but from 1970 a helicopter was used. Prior counts were carried out on foot using large numbers of beaters, the first being organized in 1929 by a visiting American zoologist, Herbert Lang. Further ground counts were conducted by the veterinary department in 1932 and 1936. There were also two early aerial counts in 1948 and 1953.

The standard technique used in the fixed-wing aircraft surveys was to fly parallel strips 1100 m apart. A four man team was used, including a pilot, recorder and two observers. Complete coverage of the game reserve area and its immediate environs required about three days (Vincent 1969). Helicopter surveys entailed intensive low altitude searching of successive blocks. Ground counts used lines of beaters walking in parallel. This technique was retained for the northern hilly section of Hluhluwe Game Reserve, where aerial coverage was difficult.

All of these survey techniques have inherent errors, which must be reconciled before the rate of increase of the white rhino population can be established. In 1970 a survey by fixed-wing aircraft carried out a week after the first helicopter census recorded only 54% of the number of rhinos obtained from the helicopter. However, the total obtained from this fixed-wing aircraft survey was also lower than that obtained in the fixed-wing censuses over the previous two years. The totals recorded in 1968 and 1969 averaged 58% of the mean number of white rhinos counted by helicopter in 1970 and 1971. Allowing for some natural increase over this period, it will be assumed that censuses by fixed wing aircraft account on average for 60% of the number of white rhinos recorded in helicopter surveys. It will furthermore be assumed that any tendency to undercount in helicopter censuses is negligible. Melton (1978) found that flying speed in helicopter surveys influenced the number of medium-sized ungulates counted, but not the white rhino totals. Since ground counts were accomplished with large numbers of beaters and covered most of the area inhabited by white rhinos at the time, it is unlikely that many rhinos were missed, so they will be assumed to be 100% efficient.

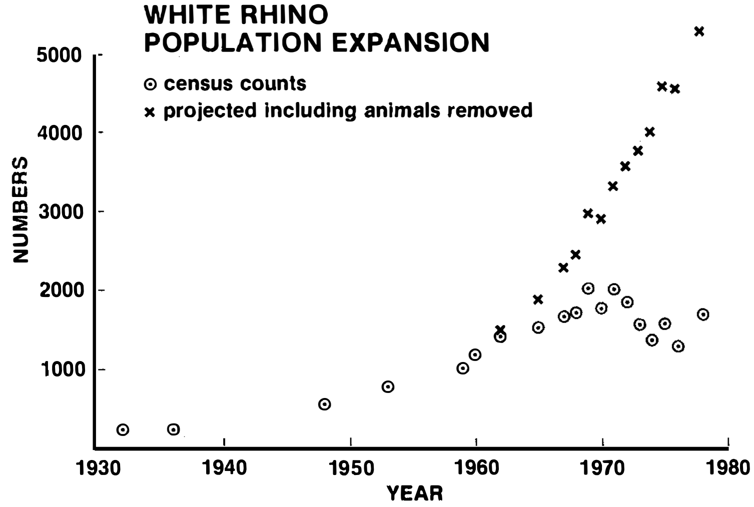

Fig. 11.1 Expansion of the white rhino population in the Umfolozi–Corridor–Hluhluwe complex, showing also the projected increase when animals removed from the population are included.

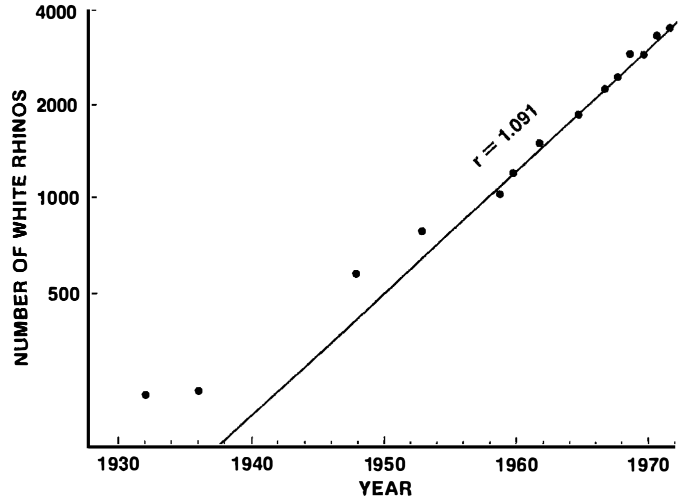

Fig. 11.2 Logarithmic plot of the projected expansion of the total white rhino population up to 1972.

Table 11.8. *Estimates of rates of increase by the white rhino population in the Umfolozi–Hluhluwe complex over different time periods*

Census method	Period	Instant. increase rate *r*	Std. error for *r*	Finite increase rate *R* (% p.a.)	95% confidence limits for *R*
All aerial censuses	1960–72	0.0917	0.0032	9.6	8.9–10.2
Early ground and air counts	1932–59	0.0611	0.0043	6.3	5.5–7.1
Fixed-wing aircraft counts	1965–69	0.1119	0.0126	11.8	9.4–14.3
Helicopter counts	1970–78	0.0622	0.0101	6.4	4.3–8.6

Allowance also needs to be made for the white rhinos translocated from the population from 1962 onwards, and for the potential recruitment to this segment. Details of the animals removed and the areas from which they were taken are documented in Natal Parks Board files. A higher proportion of subadults was removed than present in the overall population. Nevertheless it will be assumed that this segment would have increased at a rate similar to that shown by the overall population, i.e. at about 10% per annum.

The growth of the white rhino population in the Umfolozi–Hluhluwe complex is shown in Fig. 11.1, together with its projected expansion including animals removed. A logarithmic plot of the projected expansion shows a constant exponential rate of increase of 9.6% per annum over the period 1960–1972 (Fig. 11.2). Prior to 1959, the rate of increase was somewhat lower at about 6.3% per annum. Helicopter counts carried out over the period 1970–1978 also indicate a rate of increase of 6.4% per annum (Table 11.8). However, over this latter period there had been considerable disruption of the population by the greatly stepped-up capture and removal operations.

The proportion of calves less than a year old recorded in fixed-wing aircraft surveys averaged 9%, but very small calves are easily missed. Helicopter censuses over 1972–74 yielded between 10% and 14% subyearling calves, the higher figures being obtained after heavy disturbance of the population structure. A horseback survey in 1974 showed a proportion of 10% to be calves under a year old (Brooks 1974). These figures suggest a rate of increase of 8–9% per annum, allowing for a mortality rate among animals older than a year of about 2% per annum (Chapter 8).

Redistribution of the population as it expanded is evident from regional

Table 11.10. *Summary of the demographic parameters of the Umfolozi white rhino population as estimated for 1969–1970*

			Subadults				
	Adults		Post-pubertal		Pre-pubertal	Calves	
	♂	♀	♂	♀		Juvenile	Infants
Age range (years)	10–45	7–45	6–10	6–7	2.5–6	0.5–2.5	0–0.5
Proportion of population (%)	20.5	25.6	7.7	3.0	21.4	21.9	
Annual mortality (%)	3.0	1.2	3.0			3.5	8.3
Annual natality (%)	—	40.0	—	0	—	—	—
Annual dispersal (%)	3.0	0	7.5			0	

1897. After 70 annual iterations, the size of the simulated population had grown to 12 500 animals, and its rate of increase had stabilized at 9.0% per annum (allowing no dispersal).

The model population stabilized in age structure with reproductively active adults constituting 43.5% of the total. This is slightly lower than the proportion of adults estimated for the real 1969 population (46%). The discrepancy can be accounted for on the basis that the real population had not attained a stable age distribution, since its rate of increase had been lower prior to 1959. This difference in age structure would explain half the difference between the rate of increase shown by the simulated population, and that recorded for the real population, over the period 1960–72.

In the simulated population, animals in the terminal age class of 45 years formed only 0.3% of the total population. This emphasizes one factor responsible for the low mortality rate recorded in the real population – the small number of animals reaching senility. Individuals dying of senescence in 1970 would have been born during the 1920s, when the total population numbered only about 200 animals. If 20 calves had been born in 1925, and had experienced the mortality schedule shown in Table 11.10, only 7 would remain to die of old age in 1970. This may be compared with the total mortality of 18 adults estimated for the real 1969 population. This suggests that the mortality rate of prime adult females was only about 0.5% per annum, and that of prime-aged males about three times as high.

Summary

Available data suggest the following maximum sustained rates of population growth for megaherbivores: (i) elephants – about 6.5% per annum; (ii) rhinoceroses – about 9% per annum; (iii) hippopotamus – about 11% per annum; (iv) giraffe – up to about 12% per annum, depending on predation levels. Higher rates of density increase may be shown where births are augmented by immigration, and where the population age distribution has not stabilized. The rate of population growth by white rhinos at Umfolozi apparently increased with increasing density, until disrupted by large-scale removals.

Population density and biomass

The population densities attained by different large herbivore species indicate their relative success in converting plant biomass into animal biomass in particular habitats. Regional densities assessed over geographic areas, including zones where the species may be absent, need to be differentiated from local (or ecological) densities, based on occupied habitats. Furthermore short-term concentrations should be distinguished from the year-round mean densities. To compare species of different size, numerical densities need to be converted into biomass units. If a wide range in body size is represented, it is more meaningful to make comparisons in terms of metabolic mass equivalents, i.e. body mass to the power three-quarters. The metabolic mass equivalent is an index of the total energy turned over through the population.

Elephants

Elephant population density varies widely in different parks in Africa (Table 11.11). Highest regional densities of over 3 elephants per km^2 (over 6000 kg km^{-2}) occurred formerly in the Luangwa Valley in Zambia and in the North Bunyoro region of Uganda. However, in the North Bunyoro region the density had been raised by compression from surrounding human settlement, and the elephant population was in a stage of decline. Local density was 5.5 per km^2 (about 11 000 kg km^{-2}) at Manyara in Tanzania, and over 4 per km^2 in the Addo Park in South Africa. Both of these populations were still increasing. On the alluvial soils bordering the Luangwa River, elephants attained densities of 7 per km^2 during the wet season. Dry season densities along the Chobe river frontage in Botswana also reach about 7 elephants per km^2. Highest elephant densities are

regional giraffe density is 0.2 per km^2 (Hirst 1975; Leuthold & Leuthold 1978; Pellew 1983a).

Rhinoceroses

The density of Indian rhinos in Chitwan National Park in Nepal averaged 0.3 per km^2 over the total area of 907 km^2, about 70% of which was unsuitable habitat. Highest local densities reached 4.8 per km^2 (5750 kg km^{-2}). In the Kaziranga Park in India, Indian rhino density averaged 1.5 per km^2 over an area of 400 km^2 (Laurie 1978).

Black rhinos in Tsavo East in Kenya formerly had a mean density of 0.3 per km^2, with the highest local density reaching 1.6 per km^2 (1200 kg km^{-2}) over an area of 544 km^2. The black rhino population in the Hluhluwe Reserve (215 km^2) peaked at 1.4 per km^2 in 1961, but declined to 0.9 per km^2 by 1980. Elsewhere black rhino densities are considerably lower: 0.3 per km^2 at Ngorongoro, 0.17 per km^2 at Olduvai, 0.04 per km^2 at Serengeti (all in Tanzania), 0.14 per km^2 at Mara in Kenya, and 0.01 per km^2 at Etosha in Namibia (Berry 1980; Frame 1980; Goddard 1967, 1969; Hitchins & Anderson 1983).

White rhinoceros

Based on the results of helicopter censuses, the total white rhino population in the Umfolozi–Corridor–Hluhluwe complex in 1970–71 was 2000 animals over an area of 940 km^2, i.e. a regional density of 2.1 per km^2 (2800 kg km^{-2}). In Umfolozi Game Reserve alone, 1530 white rhinos occurred at a mean density of 3.2 per km^2 (4300 kg km^{-2}). Densities in the Corridor averaged 1.4 per km^2, and those in Hluhluwe 0.4 per km^2.

Within the study areas, local population densities and structure were estimated using the 'Territory Occupancy Index'. Since dominant territorial bulls were always present within the bounds of their own territories, they represented known animals occupying discrete areas. Populations of other animals within the territories were estimated from ratios of sightings compared with those of the territorial bull. Calculations are analogous to those made in the mark–recapture method of population estimation (see Caughley 1977). In the three study areas located in the western section of Umfolozi, the local population density of white rhinos averaged 5.7 animals per km^2, equivalent to a biomass of about 7600 kg km^{-2} (Table 11.4).

Summary

African elephants and white rhinos attain local population densities exceeding 5 animals per km^2 in favorable habitats. These are below equilibrium densities, since populations were still increasing. Elephant biomass may exceed 6000 kg km^{-2} on a regional scale, and 10 000 kg km^{-2} on a local scale; while white rhinos at Umfolozi attained biomass levels of over 4000 kg km^{-2} regionally and 7500 kg km^{-2} locally. Indian rhinos show local densities approaching those of white rhinos. Hippos attain ecological densities as high as 10–20 per km^2, equivalent to a biomass of 10 000–20 000 kg km^{-2}, at which levels populations appeared to be stable. Population levels attained by browsing black rhinos and giraffe are considerably lower, up to 1500 kg km^{-2}.

Comparisons with smaller ungulates

The age composition of megaherbivore populations is similar to those typical of populations of medium-sized ungulates, if age classes are defined in functional terms. In stable populations, socio-sexually mature adults generally form 60% or more of the population; while in rapidly increasing populations adults make up 50% or less of the population. Most medium-sized ungulates show an adult sex ratio bias in favor of females. While local populations of elephants and rhinos may have an excess of females, the overall sex ratio calculated over the complete distribution range tends to be close to parity.

Megaherbivore populations can sustain maximum rates of growth of 6–12% per annum. For medium-sized ungulates breeding annually, population growth rates can be as high as 25–30% per annum, if predation is negligible. However, predation normally slows the population growth of medium-sized ungulates, and also giraffe, while other megaherbivores are limited only by food availability.

Under favorable conditions, medium-sized ungulates may attain biomass levels comparable to those of megaherbivores. For example, wildebeest attained a regional biomass exceeding 7000 kg km^{-2} in the Serengeti (Sinclair 1985), while the local biomass of African buffalo at Manyara is almost 10 000 kg km^{-2} (Mwalyosi 1977). However, biomass levels exceeding 2000 kg km^{-2} are exceptional for medium-sized ungulates, but typical of megaherbivore populations allowed to reach saturation densities. Differences in metabolic mass equivalent are less marked, due to the decrease in metabolic rate per unit of body mass with increasing body size. For equivalent biomass levels, megaherbivores are represented by far fewer animals per km^2 than is the case for medium-sized ungulates.

Elephants

African elephants feed on plants by plucking grasses, forbs and creepers, frequently uprooting them; by stripping leaves, fruits, twigs or bark from woody trees and shrubs; by breaking branches off to facilitate consumption of edible parts; and by pushing over or uprooting trees and shrubs, sometimes but not necessarily always to gain access either to shoots in higher levels of the canopy or to roots. The consequences of this utilization vary depending on the species selected, the levels of damage inflicted, season at which it occurs, elephant densities, the period over which impact is sustained, and the interactive effects of other factors such as fire, rainfall and soil properties.

Changes in the species composition of woody vegetation brought about by elephant feeding have occurred where direct or indirect mortality was inflicted on certain favored species. In the Sengwa Research Area in Zimbabwe, the dominant tree and shrub species in the riverine woodland were originally *Acacia tortilis* and *Grewia flavescens.* As elephants increased in numbers, these two species declined in representation, due to felling and debarking in the case of *A. tortilis*, and uprooting in the case of *G. flavescens.* At Lake Manyara in Tanzania, mature *A. tortilis* trees were being killed by elephants at a rate of 8% per annum, and saplings at a rate of 3% per annum, over 1975–79; but recruitment by surviving saplings was regarded as adequate to maintain the tree population. Heavy culling of elephants and impala in the Nuanetsi region of Gonarezhou National Park, also in Zimbabwe, resulted in abundant regeneration by *A. tortilis* in the riverine fringe. Plants grew to a height of 5–7 m in height within 7 years (Anderson & Walker 1974; Cumming 1981a; Mwalyosi 1987).

Populations of *Acacia* spp have been depressed due to felling, debarking or uprooting by elephants in other parts of Africa. In the Seronera region of the Serengeti Park in Tanzania, *Acacia tortilis* trees were declining at a rate of 6% per annum. However, regenerating plants less than 1 m in height were abundant and ignored by elephants. Other species declining as mature trees in this park due to elephant impact included *A. xanthophloea* (5.5% per annum) and *A. senegal* (2.6% per annum). At Tsavo East in Kenya, *Acacia tortilis* plants greater than 1 m tall declined in density by 65% between 1970 and 1974, but regenerating plants less than 1 m remained abundant. At Kidepo in Uganda, the predominant *Acacia gerrardii* suffered a 23% decline among large trees over a 3 year period, while *A. senegal* also decreased markedly. In this area small trees less than 1 m were uprooted and eaten by elephants. However, other factors besides elephants were responsible here for some of the mortality among mature trees. *Acacia nigrescens* has suffered heavy elephant impact by debarking and felling in Kruger Park in South Africa, Chobe and Tuli in Botswana, Sengwa in Zimbabwe and Luangwa in Zambia. Along the Ruaha and Magusi Rivers in the Ruaha Park in Tanzania, *Acacia albida* declined in density from 8–13 per ha to about 2 per ha over 11 years, largely due to bark removal by elephants. In the Luangwa valley in Zambia, elephants felled some stands of *A. albida*, while other stands remain only lightly affected. At Mana Pools in the Zambezi valley, tall *A. albida* tress have persisted with relatively little mortality for some 20 years since bark damage by elephants was first reported. However, regeneration of this species has been suppressed completely by elephant feeding on small plants. At Amboseli in Kenya, the loss of 90% of large *A. xanthophloea* trees over a 17 year period was due primarily to an upward shift in ground water levels resulting in increased soil salinity, rather than to elephant damage. However, in the Arusha Park in Tanzania moribund *A. xanthophloea* trees were attacked more frequently by elephants than healthy trees (Barnes 1985; Croze 1974b; Field & Ross 1976; Harrington & Ross 1974; Lamprey *et al.* 1967; Leuthold 1977d; Pellew 1983c; Vesey-Fitzgerald 1974; Western & van Praet 1973; personal observations).

The baobab *Adansonia digitata* is a tree species widely susceptible to elephant damage, due to its soft, pithy wood. Elephants strip off bark, then gouge deepening holes into the trunk, until eventually the tree collapses (Fig. 12.1). Declines in baobab populations have occurred widely where elephants have reached densities that have resulted in a shortage of food during the dry season. In the Tsavo East Park in Kenya, baobabs had been virtually eliminated by 1974, less than 20 years after first reports of damage by elephants. At Ruaha in Tanzania, baobab tree density declined from 72 per km^2 to 40 per km^2 over an 11 year period, a mean rate of decrease of 3% per annum. Few trees less than 2 m in girth survived. At Lake Manyara in Tanzania, damage to baobabs was light in 1969, but by 1981 only 13% of trees remained undamaged. Annual tree mortality there was about 1% per annum. However, extinction of baobabs was unlikely, as many trees occurred on steep slopes of the escarpment where they were inaccessible to elephants. Along the Zambezi River frontage at Mana Pools, 24% of baobabs had been killed by elephant damage (15% during one year), while away from the river 6% of trees were severely damaged although few were dead. *Sterculia* spp, which like baobabs have soft trunks, have suffered similar declines at Tsavo and Luangwa (Barnes 1980, 1985; Leuthold 1977d; Napier Bax & Sheldrick 1963; Swanepoel & Swanepoel 1986; Weyerhaeuser 1985).

Fig. 12.3 Stand of *Colophospermum mopane* converted to shrub coppice form as a result of sustained elephant browsing (Luangwa Valley, Zambia).

Combretum/Commiphora thickets at Sengwa, *Lonchocarpus laxiflorus* shrublands at Murchison Falls, and *Combretum obovatum* thickets at Luangwa valley (Anderson & Walker 1974; Laws, Parker & Johnstone 1975; Penzhorn, Robbertse & Olivier 1974).

In evergreen forest patches in Uganda, elephants feed selectively on regenerating saplings of valuable timber species such as *Khaya* (mahogany), *Chrysophyllum, Cordea* and *Maesopsis.* This leads to dominance of the mature tree layer by *Cynometra* (Laws 1970; Laws, Parker & Johnstone 1975).

In some areas elephant impact has been such as to transform woodlands into open grassland. A striking example is the Rwindi–Rutshuru plain in the Virunga National Park in Zaire, as documented by paired photographs taken in 1934 and 1959 (see Bourliere, 1965, but fire was a contributory factor). In the Masai Mara Park in Kenya, fire was primarily responsible for the conversion of *Acacia* woodland into open grassland, but elephants exerted a secondary effect by browsing the *Acacia* regrowth. In the Murchison Falls Park in Uganda, the *Terminalia/Combretum* woodland was virtually eliminated in the central zone south of the Nile River. Tree density declined from between 430 and 1060 per km^2 in 1958 to 20 per km^2 in 1967. Tree death followed bark stripping by elephants, with damaged trees becoming infested with woodborers, and eventually killed by fire. At Chizarira in Zimbabwe, a *Brachystegia* woodland with a tree density of 1180 per km^2 was transformed into a lightly wooded grassland. At Tsavo East in Kenya, *Commiphora*-dominated thicket has been transformed into open savanna with scattered trees over an area of about 4400 km^2. However, these extreme habitat transformations have generally been associated with exceptional conditions. Both at Murchison Falls and at Chizarira, elephants were compressed into the sanctuary of the park by human occupation and hunting in their former range. Removal of grass by annual fires during the dry season forced elephants to concentrate their feeding on remaining woody vegetation. At Tsavo, human disturbance forced elephants to concentrate in an area with a mean annual rainfall of only 400 mm. Woodland destruction was exacerbated by severe droughts (Bell 1981a; Buechner & Dawkins 1961; Cumming 1981a & b; Dublin 1984; Laws, Parker & Johnstone 1975; Leuthold 1977d; Myers 1973; Parker 1983; Pellew 1983c; Phillipson 1975; Thompson 1975).

Nevertheless, elephants have induced declines in tree populations even in areas where they occur at relatively low densities. In the Kruger Park, with a mean density of 0.4 elephants per km^2, bark damage and felling of trees such as *Sclerocarya birrea* and *Acacia nigrescens* has been a source of concern. During two successive drought years over 1982–83, many trees suffered extensive damage, including *Combretum apiculatum, Acacia nigrescens, Adansonia digitata* and *Kirkia acuminata.* In the Seronera area of the Serengeti Park, *Acacia tortilis* trees were depressed from 48% to 3% of the total population of mature trees by a local density of elephant bulls of only 0.2 per km^2 (Coetzee *et al.* 1979; Pellew, 1983c; van Wyk & Fairall 1969; unpublished National Parks Board reports).

Large-scale reductions in elephants in Uganda resulted in a dramatic recovery by woody vegetation. At Murchison Falls, *Acacia sieberiana* trees grew to a height of 7–10 m over 24 years in plots from which elephants were excluded. One plot that had formerly been open grassland with widely scattered *Acacia* trees became transformed into close canopy *Acacia sieberiana* woodland. Associated with this change was an extreme build-up in soil nitrogen, and the herb layer became dominated by two forb species. With elephant browsing excluded, plant species richness declined from 45 to 22 species in the herb layer, and from 18 to 13 species in the tree layer. However, where *A. sieberiana* had replaced former *Combretum-Terminalia* woodland, plots showed overall increases in species richness. In the Queen

Elizabeth Park, *Euphorbia candelabrum* trees declined at a rate of 5.7% per annum over 1971–76 due to elephant damage, although low scrub regeneration was abundant. Following a drastic reduction in elephants, there was widespread regrowth by *E. candelabrum, Acacia sieberiana, A. gerrardii, A. hocki* and *Croton macrostachyus*, as well as by the shrubs *Securinega virosa* and *Turraea robusta*. In the Tsavo Park in Kenya, there was abundant regeneration by *Melia* and *Commiphora* in 1978, aided by above-average rainfall (Croze, Hillman & Lang 1981; Eltringham 1980; Hatton & Smart 1984; Laws, Parker & Johnstone 1975; Lock 1985; Smart, Hatton & Spence 1985).

Elephants serve as the prime dispersal agent of the seeds of many trees, especially in primary rain forest (Alexandre 1978; Bainbridge 1965).

Tree damage by Asian elephants is relatively light in the small parks in Sri Lanka where they are conserved. At Ruhunu, the main impact is in terms of distortion of the crown patterns of trees. At Gal Oya, about 25% of woody plants were damaged, but most of this (78%) took the form of stem or branch breaking or twisting. Only 8% of damage consisted of tree felling. Bark stripping from main trunks was rare, due to the lack of tusks of most of the elephants (Ishwaran 1983; Mueller-Dombois 1972).

Hippopotamus

Areas heavily grazed by hippos became converted from a medium-tall grass cover to a mosaic of tall and short grass areas, or even to extensive areas of short grass lawns. Terrace erosion may be evident, while bush density may increase due to the reduction in fires. On the Mweya peninsula in Queen Elizabeth Park, Uganda, palatable taller grass species such as *Themeda triandra, Heteropogon contortis* and *Cenchrus ciliaris* disappeared, except in grazing enclosures, and were replaced by the tussock-forming, relatively unpalatable *Sporobolus pyramidalis*, and by creeping *Chrysochloa orientalis*. On parts of the area erosion had removed 3–8 cm of sandy topsoil, and one erosion gully advanced 7 m over four years (Laws 1968b; Laws, Parker & Johnstone 1975; Naylor *et al.* 1973; Olivier & Laurie 1974; Petrides & Swank 1965; Thornton 1971).

Following the complete removal of hippos from the Mweya peninsula in 1958, *Sporobolus pyramidalis* increased, while *Chrysochloa orientalis* decreased. *Cynodon dactylon*, another creeping grass, almost vanished from the localities where it had formerly been common, but increased in other places. Another medium-tall grass, *Chloris gayana*, became the second-most common species, while *Cenchrus ciliaris* changed little in abundance. The basal cover of grasses declined over the first year from 15% to 5% (associated with rainfall that was only 60% of the mean), but then recovered partly to 11%. By 1975 the hippo population had recovered to a density of 25 per km², somewhat higher than the pre-1958 level. The grass community remained dominated by *Sporobolus pyramidalis*, with no further deterioration occurring. It seems that the earlier degradation was due largely to a seven year period of well below average rainfall. Nevertheless the more favorable species of taller grass, including *Hyparrhenia filipendula, Heteropogon contortis, Cenchus ciliaris* and *Themeda triandra*, predominated only in plots from which hippos were excluded (Lock 1972; Thornton 1971; Yoaciel 1981).

Giraffe

In the Serengeti Park in Tanzania, giraffe browsing reduced the growth of regenerating *Acacia tortilis* saplings to one third of that in adjacent exclosure plots. As a result, the time taken for *A. tortilis* plants to grow above 3 m in height, i.e. beyond fire-susceptible height classes, was retarded from 8 years to 21 years; while for *A. xanthophloea* it was retarded from 4 years to 19 years. At Serengeti, Kruger Park and other areas of high giraffe density, mature plants of favored *Acacia* species have their canopy shapes moulded into conical or hour-glass shapes by giraffe browsing pressure concentrated in the height range 2–4 m above ground. In the Hluhluwe-Umfolozi Reserve in South Africa, severe canopy distortion of *Ziziphus mucronata* trees was recorded, even though the density of giraffe was only about 0.2 per km² (Brooks & Macdonald 1983; Pellew 1983c).

Rhinoceroses

Indian rhinos seem to have little impact on the vegetation of Chitwan National Park in Nepal, at their prevailing density. Sumatran rhinos break down woody saplings up to 100 mm in diameter by walking over them; while males damage saplings up to 20 mm diameter by twisting them down with their horns prior to squirt-urination. However, at their low densities the impact on the vegetation is inconsequential.

Black rhinos concentrate their browsing on woody scrub under 1 m in height, especially acacias. Over half of the above-ground parts of plants in this height range may be consumed. Spindly *Acacia* saplings up to 3.8 m in height may be pushed over breaking the stem. The growth of browsed plants is retarded and some are killed. Black rhinos confined at Addo at a density varying between 1.3 and 5.2 per km² transformed a dense shrub thicket into open dwarf shrubs in a time span of a few years. In most areas black rhino densities appear insufficient to halt recruitment to taller size classes, at least in the absence of fire (Borner 1979; Hall-Martin, Erasmus & Botha 1982; Hitchins 1979; Hubback 1939; O'Regan in preparation; Vesey-Fitzgerald 1973).

White rhinoceros

When the Natal Parks Board assumed control of Umfolozi Game Reserve in 1952, *Themeda triandra* was the predominant grass species, growing in luxuriant medium–tall stands. In 1969, *Themeda*-dominated grass communities still covered 53% of the reserve area, but only 13% remained in 'climax' condition. Short grass communities characterized by creeping *Panicum coloratum* occurred over 17%, while other short or sparsely growing communities covered a further 30% of the reserve. Marked changes in grassland condition took place over the period of my study. Large sections that had been tall *Themeda* grassland in 1966 had become converted to short *Panicum–Urochloa* grassland by 1969 (Figs. 12.4 and 12.5). While the eastern slopes of the Madlozi valley had been well grassed in 1966, by 1969 they retained only a patchy grass cover with sheet erosion prominent (Figs. 12.6 and 12.7). The alluvial soils bordering the Madlozi stream has mostly tall grass in 1966, but by 1968 retained only a sparse cover of short grasses and forbs. While drought contributed to the grassland decline, the grazing impact of white rhinos and other larger herbivores was strikingly evident from a comparison of grassland condition inside and outside exclosure plots (Fig. 12.5). Since white rhinos formed over half of the total biomass of large herbivores, grassland changes could be ascribed largely to their grazing pressure. Furthermore, large-scale influxes of wildebeest and zebra into the Madlozi area took place only in 1968 (Downing 1972; Owen-Smith 1973).

In 1970, about one third of my Madlozi study area in the western section of Umfolozi was covered by short grass grassland, and much of the *Themeda*-dominated grassland was grazed down by the end of the dry season. Sheet erosion was prominent in sparsely-grassed areas, while erosion gullies had expanded in extent. Watercourses consigned chocolate-brown topsoil into the two Umfolozi rivers. The White Umfolozi, formerly a clear stream meandering over a sandy bed, had become as murky as the Black Umfolozi, and ceased surface flow for increasingly long periods during the dry season. The Black Umfolozi, formerly a fairly swift river with a rocky bed, had become silted up, and in 1970 ceased surface flow for the first time on record.

However, rainfall over the period 1966–70 was consistently below the

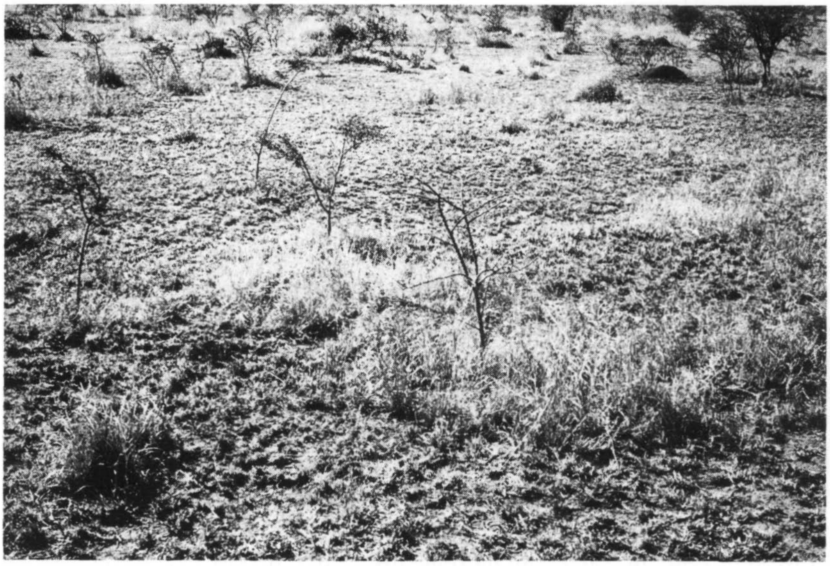

Fig. 12.4 Stand of *Themeda triandra* grassland grazed down by white rhinos, with patches of taller grass persisting around *Acacia* scrub (west of Madlozi, Umfolozi Game Reserve).

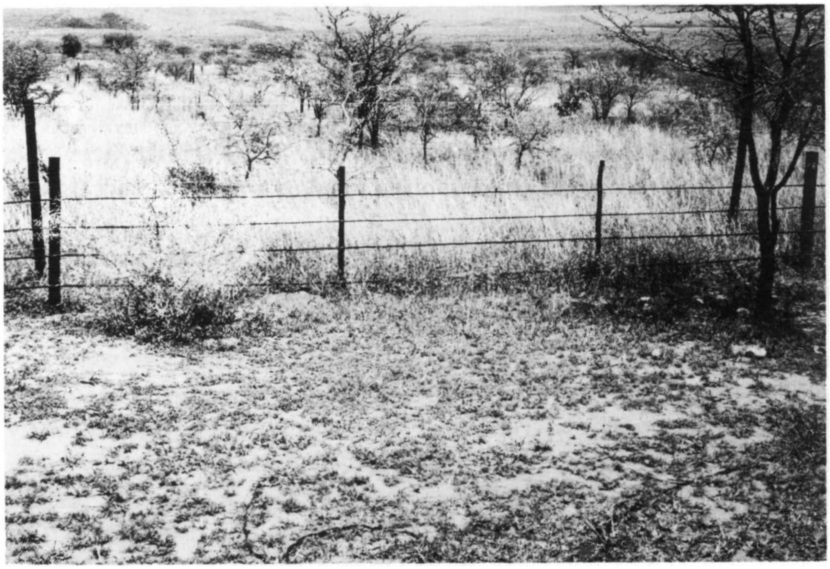

Fig. 12.5 A grazing exclosure plot south of Madlozi in Umfolozi Game Reserve, showing tall *Themeda* grassland within the exclosure, and short *Themeda–Panicum–Urochloa* grassland outside the exclosure (plot fence completed in 1967, photograph taken in October 1969).

Fig. 12.6 *Themeda triandra* grassland on the slopes of the upper Madlozi valley in Umfolozi Game Reserve in March 1966.

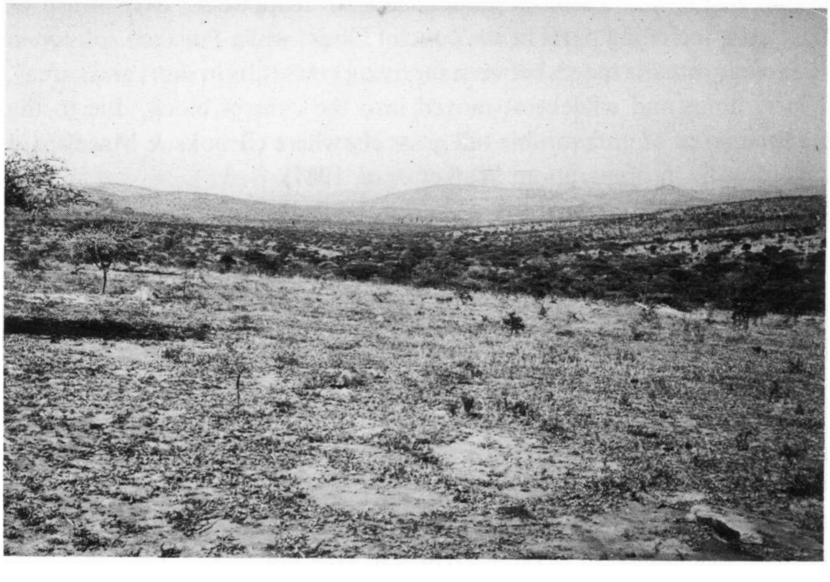

Fig. 12.7 The same view as in Fig. 12.6 photographed in August 1971, showing removal of the tall grass cover and sheet erosion.

long term average. The mid 1970s formed a period of well above average rainfall. Aided by a 30% reduction in the biomass of all grazing ungulates through culling, including white rhinos, tall grass cover improved markedly. Over 1978–83 rainfall was exceptionally low, creating perhaps 'once in a century' drought conditions. By late 1980, all tall grass reserves in Umfolozi had been grazed down, even as far as the tops of the highest hills. Short grassland areas retained only a sparse stubble, with much bare soil. Following dry season rain in 1981, an annual forb spread over much of the bare soil. Culling reduced the total biomass of grazing ungulates in Umfolozi to 60% of the 1971 level, except in a 63 km^2 control block left unculled. White rhino numbers were reduced to 40% of their 1971 total. In the control block where animal densities remained high, the grass cover declined markedly. An outbreak of harvester termites (*Hodotermes mossambicus*) removed remaining grass stubble during 1982–83, resulting in further grass mortality. Soil erosion rates increased drastically, and *Acacia* scrub 1–2 m tall became prominent in formerly open patches. The control block thus showed all the signs of extreme overgrazing, while conditions in the rest of the reserve where animal densities had been reduced were somewhat better.

During the 1983/84 season, torrential cyclonic rains resulted in a precipitation 60% above average, and rainfall remained high through 1984/85. By March 1985, tall *Themeda* grassland had reappeared over most of Umfolozi, including parts of the control block; while *Panicum coloratum* had spread into the spaces between surviving grass tufts in short grass areas. White rhinos and wildebeest moved into the control block, due to the predominance of unfavorable tall grass elsewhere (Brooks & Macdonald 1983; Emslie in preparation; Walker *et al.* 1987).

The history of grassland dynamics in Umfolozi Game Reserve over this period demonstrates a strong interactive effect between grazing pressure and rainfall. Grasslands deteriorated everywhere during periods of low rainfall, but the change was less extreme in areas protected from grazing, or where grazer densities were markedly reduced, than in areas where animal densities were left unmanaged. The major grazing impact was due to white rhinos, although other grazing ungulates such as wildebeest, zebra, impala and warthog contributed. Nevertheless, grasslands recovered following high rainfall even in areas that had appeared badly degraded, at least to the extent that they became attractive to short grass grazers. In areas where animal densities had been reduced, an excess of tall grass made conditions unfavorable for many of the ungulate species.

Summary

African elephants can exert a negative influence on populations of mature trees of sensitive species. These include species easily uprooted by felling (e.g. *Acacia* spp, *Commiphora* spp), those with bark that is easily stripped (*Acacia* spp, *Pterocarpus angolensis, Brachystegia boehmi*), and trees with soft pithy trunks (*Adansonia digitata, Sterculia* spp). Other species that respond to trunk breakage by coppice regrowth of the stump, such as *Colophospermum mopane*, persist despite severe elephant impact, although their growth form is changed. Elephants uproot and consume small woody plants, at least those taller than 0.5 m, thereby suppressing replacement of the mature trees that they kill. Under extreme conditions where elephants are crowded into small areas, they can transform wooded savanna into open grassy savanna. Woody plant damage is exacerbated following grass removal by fire or drought. In forests, elephants of both species may suppress shade-tolerant 'climax' trees by creating open gaps colonized by faster-growing species. Elephants commonly uproot grass plants while feeding, but despite this their impact on the grass layer appears negligible.

Sustained grazing pressure by white rhinos and hippos can transform medium–tall grassland areas into communities dominated by short or decumbent grass species. With reduced canopy cover, soil erosion may be accelerated, and due to reduced fire frequency woody scrub may invade grassland. Deterioration in the grass cover generally takes place in association with below-average rainfall.

Browsing pressure by black rhino and giraffe can slow or suppress the growth of regenerating woody plants. By keeping plants within the fire susceptible zone for longer, browsing may retard recruitment to mature height classes.

Effects on other large herbivores

Different species of large herbivore are potential competitors for food resources. However, competition is effective only where a food resource shared in common by two species is limiting, so that a reduction of the available food by one species depresses the population density that the other species can attain. For herbivores food quality is generally more limiting than food quantity (Sinclair 1975; Rhoades 1985). A reduction in plant biomass due to consumption by one species may improve food quality for another, by stimulating regrowth of nutrient-rich new leaves, or by making foliage more accessible (McNaughton 1976). Megaherbivores are the prime species in terms of biomass in 13 out of 16 African parks for which good census data are available (Chapter 14), as well as in those Asian parks where they remain effectively conserved (Eisenberg & Seidensticker 1976). Although the food intake of megaherbivores per unit of biomass is only about two-thirds that of medium-sized ungulates, one or other megaherbivore species is generally pre-eminent in the larger herbivore community in terms of consumptive demand.

Populations may also interact less directly. A change in the structure or species composition of the vegetation may make certain species vulnerable to predation (Sinclair 1985). Water availability may be improved, or reduced. The subject of competition remains controversial, because it is difficult to distinguish direct interactions between populations from independent responses to changing habitat conditions, which may be induced by weather fluctuations or other external causes. Experiments are difficult to perform on large herbivores, so that in general the only information available to suggest competitive or facilitatory effects consists of relative population changes over time. Such evidence must be treated with due caution. Where two populations change in antisynchrony, this suggests the possibility of a competitive interaction, but the population changes could be due to independent responses to some other environmental factor (Owen-Smith 1988 in press).

Elephants

African elephants form the greatest component of large herbivore biomass in 10 out of 16 parks, while they are second to hippos in two parks, and fall just below African buffalo in one park. Only in the grassy savanna of the East African plateau, e.g. the Serengeti and Nairobi parks, are they a minor faunal constituent.

At Tsavo East in Kenya, elephant density reached high levels before the population crash associated with the 1971 drought. The opening up of the woody vegetation that they caused was associated with declines in the populations of other browsing ungulates. Although data on population changes are unavailable for Tsavo National Park, there are figures for the neighboring Galana Ranch, where very similar habitat changes occurred. Between 1963 and 1981–82, lesser kudu declined by 90%, gerenuk by 80% and giraffe by 40%. Black rhinos decreased to very low numbers, but poaching was a contributory factor in this case. In compensation, grazing ungulates such as Grevy's zebra and oryx, as well as Grant's gazelle, increased markedly (Parker 1983). These population changes are probably a response to the opening up of *Commiphora* shrublands and riverine thickets by elephants, rather than to competition by elephants for browse. For example, black rhino show relatively little overlap with elephants in their food preferences at Tsavo (Chapter 3).

In association with a 40% increase in elephant numbers in the Ruaha Park and environs in Tanzania between 1973 and 1977, there were apparent declines by zebra, impala, eland, kudu and black rhino, while buffalo and giraffe increased. While the overall diversity of large herbivores appeared to have dropped, little reliance can be placed on these differences, which are based on only two aerial censuses (Barnes 1983a; Barnes & Douglas-Hamilton 1982; Norton-Griffiths 1975). Along the Chobe River in Botswana, opening up of *Combretum* thickets by elephants has resulted in far fewer bushbuck being seen than was the case earlier (D. Work personal communication). At Sengwa in Zimbabwe, although elephants reduced total woody biomass, there was more browse available within the height reach of medium-sized ungulates (Guy 1981). In the Kruger Park in South Africa, trees pushed over by elephants were sought out by kudus during a drought (personal observations). In the Addo Park in South Africa, numbers of browsers, in particular kudu and eland, increased following the expansion of elephants into a new section of the dense valley bushveld (A. Hall-Martin personal communication).

While elephants may derive half their food intake from the grass layer, competitive influences on grazing ungulates have not been reported. Instead, elephants may facilitate grazing by other ungulates by opening up tall grass in valley grasslands (Vesey-Fitzgerald 1960). On the other hand, by creating dense stands of woody coppice that shade out the grass layer, elephants may create unsuitable conditions for grazers such as sable and Lichtenstein's hartebeest (Bell 1981a).

Hippopotamus

Hippos are the major species in Queen Elizabeth National Park in Uganda, forming 40% of the large herbivore biomass (Field & Laws 1970; Eltringham & Din 1977). In 1958 hippos were eliminated from the 4.4 km^2 area of the Mweya Peninsula. By 1968, the total biomass formed by other large herbivores had increased three-fold. Elephant, buffalo and waterbuck showed increases, while warthog and bushbuck declined. By 1973 hippos had recovered to more than their former density. Numbers of elephant, buffalo and waterbuck using the area had dropped, while warthog numbers were unchanged. However, population changes in such a small area are unreliable. The drop in buffalo numbers was due to the breakup of one large herd using the area (Eltringham 1974, 1980).

Giraffe

Giraffe derive most of their food from levels out of reach to other browsers, and thus do not compete directly, except perhaps for fruits and pods that may otherwise fall to the ground. By retarding growth by regenerating *Acacias*, giraffe are likely to facilitate browsing by smaller ungulates (Pellew 1983c; J.T. du Toit personal communication).

Rhinoceroses

Indian rhinos are pre-eminent among wild herbivore species in biomass at Chitwan in Nepal, and are second to elephants at Kaziranga in India (Eisenberg & Seidensticker 1976). Their effects on other ungulates are unreported.

Black rhinos generally feed at a lower level than other browsing ungulates like kudu and giraffe, reducing the potential for competition with other large browsers. Since woody plants sprout soft new shoots following browsing, feeding by black rhinos may increase food quality for smaller browsers. However, they may compete for forbs with kudu, nyala and perhaps small antelope like steenbok and dikdik (Joubert & Eloff 1971; B. P. O'Regan personal communication).

White rhinoceros

When the Natal Parks Board assumed control of Umfolozi Game Reserve in 1952, other large ungulates besides rhinos had been virtually eliminated by the shooting campaign carried out by the veterinary authorities to eliminate hosts for tsetse fly. Numbers of wildebeest, zebra, buffalo, waterbuck, impala and nyala thereafter increased steadily through colonization from Hluhluwe Game Reserve via the Corridor. By 1970, the total biomass of large herbivores in Umfolozi exceeded 8000 kg km^{-2}, of which white rhino formed 50% (Table 12.1). Hluhluwe Game Reserve supported a similar biomass, but with white rhino comprising only 6%. At about this time, the Natal Parks Board vastly increased their culling quotas for all grazing ungulates, in an attempt to alleviate perceived overgrazing of grasslands. White rhino numbers in Umfolozi were reduced from 1550 in 1972 to 1070 in 1976, and 600 by 1982. Wildebeest had declined by 1982 to 30% of their 1970 peak, while numbers of buffalo, zebra and impala remained unchanged or increased despite the removals.

Table 12.1. *Ungulate populations in the Umfolozi–Corridor–Hluhluwe Complex*

Areas: Umfolozi Game Reserve (UGR) (south of Black Umfolozi River) – 456 km^2; Hluhluwe Game Reserve (HGR) – 215 km^2; Corridor (Cor) – 270 km^2; Complex – 940 km^2.

Species	estim. mean weight[a] (kg)	Estim. undercount factor	Numbers				Biomass (kg km^{-2})			
			UGR	Cor	HGR	Total	UGR	Cor	HGR	Total
White rhinoceros	1350	1.0	1361	313	90	1764	4028	1565	568	2532
Wildebeest	160	0.9	3745	2170	1159	7074	1310	1290	862	1200
Zebra	210	0.8	1027	1308	1096	3431	472	1017	1072	765
Buffalo	410	1.0	426	640	651	1717	384	974	1240	750
Impala	40	0.5	2506	4114	9850	16470	220	610	1836	700
Nyala	55	0.5	2634	696	4360	7690	318	142	1114	448
Waterbuck	155	0.67	1567	396	39	2002	532	228	28	330
Kudu	165	0.67	1260	85	331	1677	457	52	253	295
Warthog	40	0.5	3346	1138	1762	6246	294	170	328	264
Black rhinoceros[b]	700	—	60	69	199	328	91	179	647	246
Giraffe	800	1.0	17	0	17	34	30	0	63	29
Reedbuck	45	0.5	946	76	10	1032	92	6	—	48
Mountain reedbuck	30	0.5	218	8	20	246	14	—	—	8
Total							8242	6239	8011	7615

Notes: Not censused: bushbuck, bushpig, grey duiker, red duiker, eland, klipspringer, steenbok, blue duiker.

[a] Equals $\frac{3}{4}$ of average adult weight for most species; for white rhinoceros based on known age structure; weights from Hitchins (1968), Wilson (1968), Smithers (1971).

[b] Not censused, populations from Hitchins (personal communication 1971).

Sources: Derived from the Natal Parks Board helicopter census of August 1970 (Vincent 1970), with corrections for undercounting bias (modified from Melton 1978).

Only half of the decrease by wildebeest could be accounted for in terms of removals. Three other ungulate species declined in numbers in Umfolozi subsequent to 1970, although not subjected to culling. By 1982 common reedbuck numbers had dropped to about 15% of their 1967 abundance, bushbuck to about 25% of their 1967 abundance, and waterbuck to about a quarter of their 1970 numbers. Wildebeest may have been influenced adversely by the increase in tall grass during the 1970s, but an increase by lions was probably also a contributory factor. Waterbuck may have been under stress from the earlier reduction in tall grass cover caused by the increasing grazing impact of white rhino, although other factors such as higher tick loads and greater predator numbers were probably contributory factors. Reedbuck almost certainly suffered from the opening up by white rhino grazing of the tall grass cover that they depend on as a refuge from predation. In the case of bushbuck, competition from the expanding nyala population has been invoked; but they were probably also influenced adversely by the opening up of vegetation cover in bottomland regions, to which white rhinos contributed. Thus the only species that suffered adversely from the vegetation impact of the high white rhino biomass were reedbuck and, more equivocally, waterbuck and bushbuck (Brooks & Macdonald 1983).

Summary

Megaherbivores are generally pre-eminent in terms of biomass in large herbivore communities occupying African savanna. Their consumptive demands therefore have a greater impact on vegetation than that of other large herbivore species in the community, while they exert additional vegetation impact through breakage and trampling. Megaherbivores do not compete directly to any significant extent with other larger herbivore species. However, the vegetation changes that they induce may affect other herbivore species. By opening up thickets, elephants reduce cover for species such as bushbuck, but increase browse availability for other species. By transforming stands of tall grass into short grass, white rhinos and hippos may exert a negative influence on ungulate species dependent upon taller grass for either food or cover; but such grassland changes may be beneficial for species favoring short grass. However, by generally promoting the replacement of tall mature woodlands or grasslands by rapidly growing shrubs or short grasses, high megaherbivore densities are more likely to favor than be to the detriment of smaller species of herbivore.

Comparisons with smaller ungulates

Wildebeest in large concentrations, such as occur in the Serengeti Park in Tanzania, can transform stands of medium-tall *Themeda* grassland into short grass. By trampling and horning, they also damage and suppress small woody plants in the grass layer. However, their grazing pressure on taller grasses is restricted mostly to the dry season, so that changes in grassland composition generally do not result (Dublin 1984; McNaughton 1984). Short grass grazers like wildebeest and impala may, by their sustained grazing pressure on short grass areas, cause progressive denudation of the grass cover. Domestic cattle at high numbers, such as are commonly stocked in African tribal areas, can certainly convert medium–tall grasslands into degraded areas of sparse short grass and encroaching bush (Lamprey 1983). Wild populations of African buffalo do not have this effect; the culling of buffalo in the Kruger Park is justified primarily in terms of their competition with other ungulate species for water (Joubert 1983). Small browsers may have a significant impact on the survival of woody plant seedlings, but effects on woody plant communities remain to be documented. Populations of wild ungulates, apart from megaherbivores, have caused major changes in African savanna vegetation only in circumstances where predators have been eliminated, or movements confined by fencing to small areas, or in the vicinity of waterpoints (Cumming 1982).

13

Body size and population regulation

Introduction

For an expanding population to be transformed into a stable one, density dependent changes must occur either in rates of recruitment, in population losses, or in both (Caughley 1977). Recruitment can decline due to (i) a decline in female fecundity, brought about by reduced litter sizes, or increased intervals between births; (ii) higher post-natal losses; or (iii) ages at first parturition being retarded. Losses can increase due to (i) increased mortality, whether as the direct result of nutritional deficiencies, or as a result of predation or disease; or (ii) to increased emigration from the area.

Caughley & Krebs (1983) suggested that there is a fundamental dichotomy between the processes of population regulation in small mammals (under about 30 kg in body mass), and those operating in larger mammals. The former are regulated mainly by intrinsic mechanisms, i.e. by behavioral or physiological responses acting before food becomes limiting. In contrast, large mammals are regulated largely by extrinsic factors, such as the direct effects of food limitations on survival and reproduction.

Goodman (1981) emphasized that the population dynamics of large, long-lived mammals are much more sensitive to variations in annual survival rates than to corresponding variations in fecundity. These circumstances favor deferred reproduction as an adaptive response to adverse conditions.

Riney (1964) maintained that populations of large herbivores expanding from low densities in favorable habitats inevitably overshoot the carrying capacity of the vegetation. He suggested that the typical pattern was an eruptive oscillation, which could be subdivided into four stages: (i) an initial phase of rapid expansion with high fecundity and low mortality, with vegetation condition beginning to deteriorate towards the end of this period; (ii) a phase of temporary stabilization as the population reaches, then exceeds, the carrying capacity of the habitat; vegetation degradation is accelerated, and animal condition declines; (iii) a phase of rapid decline in numbers as the population adjusts to a lowered carrying capacity brought about by its impact on food resources; (iv) a final phase of stabilization in the degraded habitat at a density very much lower than that reached during earlier stages. Riney proposed that the overshoot of carrying capacity was an inevitable consequence of the upward momentum built into the growing population due to the high proportion of animals in younger age classes. Thus even if age-specific fecundity and mortality rates were to adjust instantaneously to those values characterizing a stable population, the breeding segment would continue to expand for a period, due to continuing recruitment into it of those young animals already alive.

Caughley (1976a, 1977) generalized Riney's description into an analytic model of plant-herbivore systems. For plants the rate of renewal of primary resources, such as sunlight and water, is largely independent of the existing plant biomass. Under these conditions a simple logistic model of population growth is applicable. In contrast, there is an interaction between herbivore populations and the plants that form their resource base. Interactive systems tend to display oscillations in both plant and herbivore biomass, because of the lag in the effect of herbivore feeding on future vegetation growth. If in the model vegetation biomass is reduced to less than half of its potential in the ungrazed state, persistent oscillations develop. These take the form either of a stable limit cycle, or of divergent oscillations leading to the extinction of the herbivores alone, or of both herbivores and plants.

Fowler (1981) suggested that large mammals are liable to overshoot their ultimate mean population levels due to the non-linear dependence of demographic variables on population density: i.e. changes in birth rates and mortality are initiated only at population levels close to carrying capacity.

Caughley (1976b) suggested, specifically with regard to elephant populations, that no stable equilibrium with vegetation is reached. Elephants inevitably increase to densities sufficient to exert a major impact on tree populations, resulting in the death or emigration of most of the elephants. The pattern of change generated is one of a stable limit cycle with a period of about 200 years.

Other hypotheses have been advanced to explain why elephant populations fail to stabilize before severe damage to woody vegetation has been inflicted. These are:

1. Range compression. Laws (1969b, 1970) and others suggested that elephants have been forced into national parks by hunting, settlements and other human disturbances in surrounding areas.

Human activities furthermore inhibit movement by elephants out of these sanctuaries. As a result population densities reach atypically high levels.

2. Population eruption. Elephant numbers were depressed over much of Africa at the end of the last century as a result of ivory exploitation. Following the cessation of ivory hunting, populations entered a phase of eruptive expansion, which has caused them to temporarily overshoot carrying capacity (Spinage 1973).
3. Elimination of human predation. Kortlandt (1976) argued that humans have been major predators of proboscideans since the Pleistocene, possibly displacing the extinct sabretooths from this role. Pienaar (1983) suggested that the rapid expansion of elephant, hippo and buffalo populations in the Kruger Park was related to the elimination of hunting.

A pattern of herbivore populations increasing inevitably to densities at which they overexploit and depress their own food resources is inherently unstable, and seems incompatible with large, K-selected mammals like megaherbivores. To be considered in this chapter are these questions: (i) Do expanding megaherbivore populations inevitably show an eruptive oscillation? (ii) Is vegetation degradation an inevitable consequence of megaherbivore population expansion? (iii) Can megaherbivores attain a stable equilibrium with vegetation? (iv) What difference does dispersal make? (v) How do megaherbivores differ from small ungulates in processes of population regulation?

I will use simulation modelling as an analytic aid. Simulation models can be used to explore possible behaviors of a system given certain assumptions about its structure and the interactions taking place within it. Caution is advisable in extending conclusions derived from any model to the real system that the model is intended to represent. Modelling is best approached as a heuristic thought-provoking exercise.

Demographic models

I developed a computer-based simulation model intended to be sufficiently detailed to capture the essential features of the population dynamics of a large, long-lived megaherbivore like white rhino. The basis of the model is a population structured into age classes differing in their mortality, natality and emigration rates (see Appendix II). A simulation incorporating the demographic characteristics of the Umfolozi white rhino population in 1970 closely replicated the observed features of this expanding population.

Some indication of possible changes that could bring about stabilization is given by the demographic characteristics of the black rhino population in the Hluhluwe Reserve. This population had declined from a total of about 300 animals in 1961, to 199 individuals in 1972. In contrast, the black rhinos occupying the adjoining Corridor and Umfolozi Reserve seemed to be in a phase of population expansion. A comparison between the population statistics from these two regions suggests that the following changes had occurred at Hluhluwe: (i) mean calving interval lengthened from 2.3 to 2.7 years; (ii) age at first parturition retarded from 6.5 to 12 years; (iii) infant mortality increased from 9% to 59% per annum, with hyena predation largely responsible; (iv) adult mortality increased to 3.5% per annum in females and 7.3% per annum in males; (v) mortality of immature plus juvenile animals increased to 5.7% per annum (the population sample for the Corridor plus Umfolozi was too small for mortality rates of adults and subadults to be estimated) (Hitchins & Anderson 1983).

Another possible example is given by the African elephant population in the Murchison Falls National Park in Uganda. This showed a decline from an estimated 22 000 animals in 1946 to 9400 in 1966, with about half of the reduction due to control or sport hunting. Demographic changes included an increase in mean calving interval from 4 to 7 years, a retardation of female puberty from 12 to 18 years, and an increase in calf mortality from 28% to 43% (Laws, Parker & Johnstone 1975).

For white rhinos it is anticipated that the main demographic changes would occur in age at first parturition and in birth interval, and to a lesser extent in infant survival. By trial and error with the computer simulation, it was found that the following combination of changes would achieve a stationary white rhino population: (i) natality rate for prime aged females reduced from 45% to 25% per annum; (ii) natality of old females reduced from 25% to 15% per annum; (iii) age at first calving retarded from 6 years to 10 years; (iv) infant losses tripled from 8% to 24%; (v) juvenile mortality increased from 3.5% to 8% per annum; (vi) subadult mortality increased from 3% to 6% per annum; (vii) mean mortality of prime adults doubled from 1.5% to 3.0% per annum; (viii) mortality of old animals (over 35 years) increased to 8% per annum. In the model stationary population, 58% of the animals are adults (> 10 y), 27% are subadults (3–10 y), and 14.5% are calves (0–3 y). Infants under one year of age form 5.2% of the population, compared with 11% in the real population in 1972. The terminal mortality of adults at the age of 45 years adds an additional amount of 1% per annum to the overall mortality rate of adults, so that this becomes 5% per annum. These characteristics suggest a white rhino population experiencing fairly severe nutritional limitations.

To make the model dynamic, density-dependent functions must be formulated for rates of natality, mortality and emigration. Furthermore, the density level at which the population stabilizes must be decided.

Since the white rhino population was still increasing at near its maximal rate in 1970, biomass levels prevailing then were evidently some way below the upper limit based on food resources. This upper limit I will term the saturation density. Considering that retrogressive habitat changes had been initiated, the saturation density cannot lie too far above the 1970 density. Arbitrarily it will be assumed that the white rhino population in 1970 was at two-thirds of its saturation density. The mean density of white rhinos over the 450 km^2 area of Umfolozi in 1970 was 3.2 per km^2, equivalent to a biomass of 4300 kg km^{-2}. Thus the assumed saturation biomass is 6500 kg km^{-2}, or a mean white rhino density over the whole extent of Umfolozi nearly as high as that prevailing in the western high density zone in 1970.

To make the model more realistic, physiological lags in responses to changing biomass levels will be allowed (supposedly related to the stored body reserves carried through from previous years). Thus the mortality and natality rates of adults and subadults become functions of mean biomass averaged over the preceding three years, juvenile mortality becomes a function of mean biomass over the preceding two years, and infant mortality of the prevailing biomass over the preceding year. Age at first parturition, because of its dependence on growth rate, will be taken to depend on mean biomass over a five year period.

In the model, dispersal is an option that can either be allowed or prevented. Other modifications will be introduced below. Results of the simulation runs were as follows:

1. Expanding population with no vegetation interaction

If the model population is started at a density similar to that of the Umfolozi white rhino population in 1925, it increases rapidly to reach the saturation biomass after 25 years (Fig. 13.1(*a*)). The population overshoots the saturation biomass by 13%, and undergoes a small oscillation before stabilizing. Thus even with the multiple time lags built into the model, the oscillation is fairly minor. Nevertheless, the peak biomass reached is 65% greater than that prevailing for the real population in 1970, when retrogressive changes in grasslands were strikingly evident.

Dispersal was prevented in the above simulation. If dispersal is allowed, at rates similar to those estimated to be occurring in the real white rhino population, the model population levels off below the saturation biomass and barely oscillates (Fig. 13.1(*b*)). The equilibrium biomass level attained is only 25% greater than that prevailing for the real population in 1970. Thus dispersal dampens oscillations and causes the population to equilibrate at a lower density than that reached in the absence of dispersal.

2. Increasing population with vegetation impact

For this simulation, the peak wet season biomass of grass is assumed to be 200 g m^{-2} y^{-1} (based on the measurements of P. Dye, 1983, in a savanna with similar rainfall at the Matopos Research Station in Zimbabwe). Of this total, 50% is assumed to be unavailable or inaccessible (e.g. on steep hillslopes); and 50% of the remainder is assumed to be eaten or otherwise removed by other herbivores, including insects such as harvester termites as well as other ungulates. Thus the amount of edible and accessible food that is available for consumption by white rhinos amounts to 50 g m^{-2} y^{-1}. From the data presented in Chapter 5, the eating rate of a white rhino is about 1.5% of body mass (dry mass/livemass) per day. Hence the total grass consumption (in dry mass) by white rhinos over the course of a year amounts to five times the standing live biomass of white rhinos.

For the grass population, a simple logistic model will be assumed. The maximum between-year growth rate of the grass population (as distinct from the within season accumulation rate of grass biomass) is taken to be 50% per annum. Agriculturalists commonly assume that the threshold for overutilization of grasslands lies at a consumption level removing about 50% of annual above-ground grass production. McNaughton (1979) showed that short grass grasslands in the Serengeti can sustain somewhat higher grazing pressures; but the graminoids in this region seem to be exceptional in their tolerance of grazing, due partly to the extremely nutrient-rich volcanic soils. In the model it will be assumed that, if white rhinos remove less than 50% of the available grass production, they have no impact on the grass population; they simply remove part of the annual growth, which is replenished completely the next season. If consumption levels exceed the 50% threshold, the grass population the following year is depressed, due to the death of some tillers or tufts (see Appendix II for the formulation of this effect). The model parameters are adjusted such that, at the saturation biomass of white rhinos, grass consumption exceeds the overgrazing threshold.

The model was re-run with identical starting conditions to those used for the model with no vegetation impact. With dispersal prevented, the output shows slowly fading oscillations by both white rhino and grass populations, with a period of 35 years (Fig. 13.1(*c*)). If emigration is allowed, the

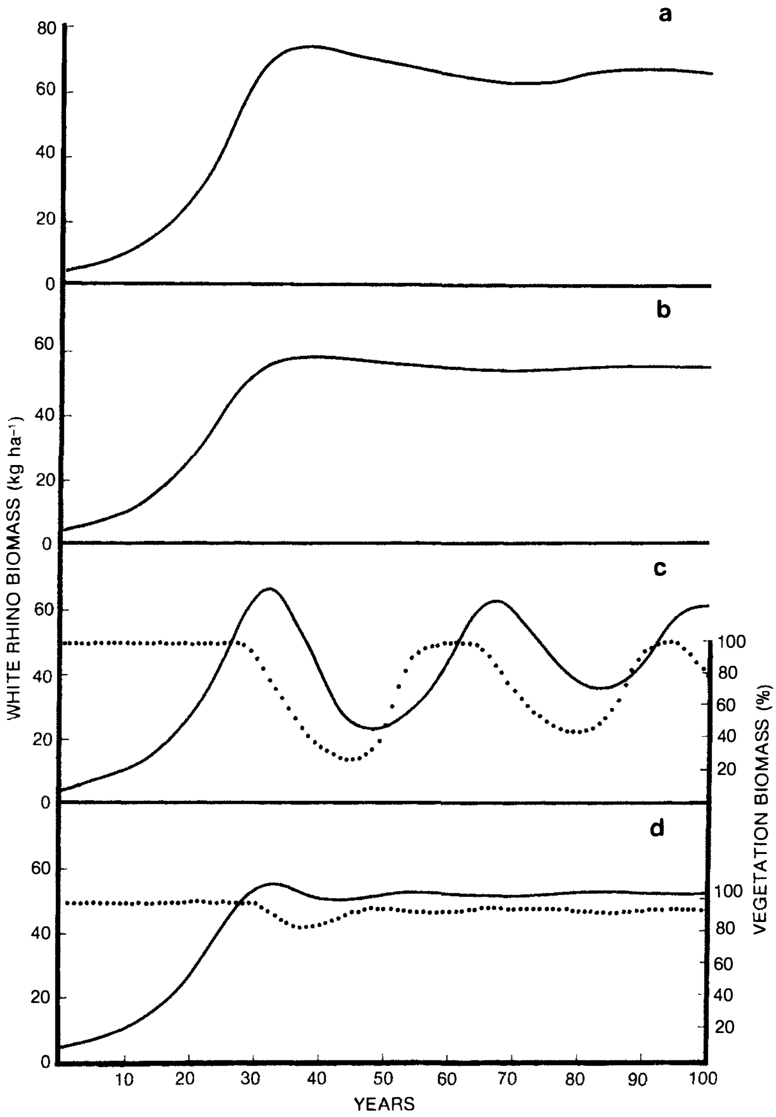

Fig. 13.1 Model output showing the pattern of increase by the simulated white rhino population under different conditions. Parameter values given in Appendix II, rainfall constant. The solid line indicates white rhino biomass; dots indicate vegetation biomass, as a percent of the maximum. (a) no vegetation interaction, no dispersal, (b) no vegetation interaction, with dispersal allowed, (c) with vegetation interaction, no dispersal, (d) with vegetation interaction, with dispersal allowed.

oscillations are dampened, because the peak density attained by the white rhino population only marginally exceeds the threshold biomass for overgrazing to be induced (Fig. 13.1(*d*)).

In general the precise behavior of the model is determined by the specific values selected for the vegetation parameters. Only very minor oscillations develop if grass production is such that the overgrazing threshold is not reached. If the potential rate of increase of the grass population is raised, the amplitude of the oscillations is reduced.

3. Fluctuating rainfall regime

This simulation investigates how an initially stabilized population of white rhinos might respond to year to year differences in rainfall. Grass production, and hence the amount of food available for herbivore consumption, can differ widely between years in association with rainfall fluctuations. Hence if the herbivore population is food-limited, its potential saturation density changes between years. For regions receiving annual rainfall totals of less than about 700 mm per year, grass production is almost linearly related to the current season's rainfall (Dye 1983). Thus in the model the saturation biomass of white rhinos becomes a variable whose value is dependent upon the seasonal rainfall total. In addition, the extent to which the grassland is overgrazed depends on the relation between the current season's grass production, which is linearly related to rainfall, and the consumptive demand of the white rhinos, which is dependent upon the prevailing white rhino biomass.

The available rainfall data for Umfolozi Game Reserve spanned a 22 year period from 1959 to 1981. In order to generate a sufficiently long time period for the model population to move away from the initial conditions, the available rainfall figures were replicated four times to yield an 88 year sequence, the last 22 years of which correspond to the real rainfall received over the period 1959–81.

When run under conditions of no dispersal, the model white rhino population fluctuates widely in biomass, rising to peaks during phases of high rainfall, such as prevailed over 1959–64 and 1973–77, and declining rapidly during phases of low rainfall, such as occurred over 1964–73 and 1977–81 (Fig. 13.2(*a*)). Because of the lag in population response, an overgrazing effect depresses grass populations at the start of each dry phase.

If dispersal is allowed, the population fluctuations are greatly reduced, although the mean population biomass is closely similar in the two simulations (4733 kg km^{-2} with no dispersal, and 4582 kg km^{-2} with dispersal

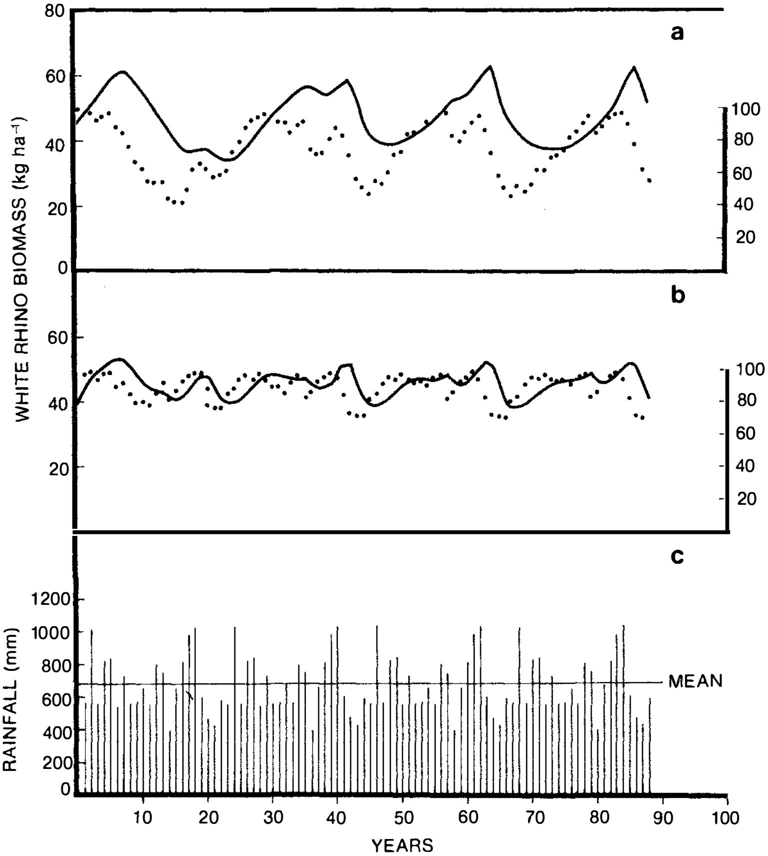

Fig. 13.2 Model output showing biomass changes by a simulated white rhino population under a variable rainfall regime, based on the Umfolozi records. The solid line indicates white rhino biomass; dots indicate simulated changes in the population of plants serving as a food resource. Parameter values given in Appendix II. (a) vegetation interaction, no dispersal, (b) vegetation interaction, with dispersal allowed, (c) rainfall pattern used in the simulation.

(Fig. 13.2(*b*)). The depression of the grass population due to overgrazing is greatly reduced.

If a model population expanding under conditions of rainfall variability is simulated, the regular pattern of the population oscillations depicted in Fig. 13.1 is disrupted. Should the initial population peak happen to coincide with a drought period, the depression of plant populations is more severe than it would otherwise be.

4. Effects of body size

In order to compare processes of population regulation in megaherbivores with those operating in smaller ungulates, the parameters of the simulation model were adjusted to represent a medium-sized antelope, such as a wildebeest. The differences in parameter values between the two versions of the model are listed in Appendix II, together with details of the changes made in formulation.

If the saturation biomass of 'wildebeest' is set at the same level as that of white rhinos, the degree of overgrazing that occurs at saturation levels is much more severe than was generated in the white rhino simulation. This is because medium-sized ungulates exhibit a higher feeding rate per unit of biomass than do megaherbivores. Such a situation simply generates a crash by the 'wildebeest' population, associated with a reduction in grass biomass to baseline levels. Hence the saturation biomass of 'wildebeest' was adjusted in the model so that at saturation they consume the same fraction of grass production as is eaten by 6500 kg km^{-2} of white rhinos in an average rainfall year.

If the model is run so as to simulate an expanding population of wildebeest with no emigration, the outcome is basically the same as that of the comparable white rhino simulation: the population increases to exceed its saturation biomass by 13%, and then undergoes dampened oscillations with a period of 16 years (Fig. 13.3(*a*)). The equilibrium biomass towards which the population tends is 25% less than the saturation biomass, because of the effect of overgrazing on the grass population. If emigration is allowed, the initial overshoot of carrying capacity is reduced to 2%, and the oscillations fade away more rapidly (Fig. 13.3(*b*)). The eventual equilibrium density is the same as that attained with dispersal prevented; but the population appears healthier in terms of the mortality rates prevailing at this equilibrium biomass.

In the model formulation, the mortality rates at saturation densities of 'wildebeest' are nearly three times as great as they are for white rhinos. The higher mortality of medium-sized ungulates can be interpreted as due largely to predation. Thus to simulate a situation without predators, a constant 5% was subtracted from the density-dependent mortality levels in each age class. With this change, the model 'wildebeest' population becomes highly unstable in the absence of emigration. It increases rapidly to a high biomass, then crashes due to grassland depletion, with oscillations tending to be sustained (Fig. 13.3(*c*)).

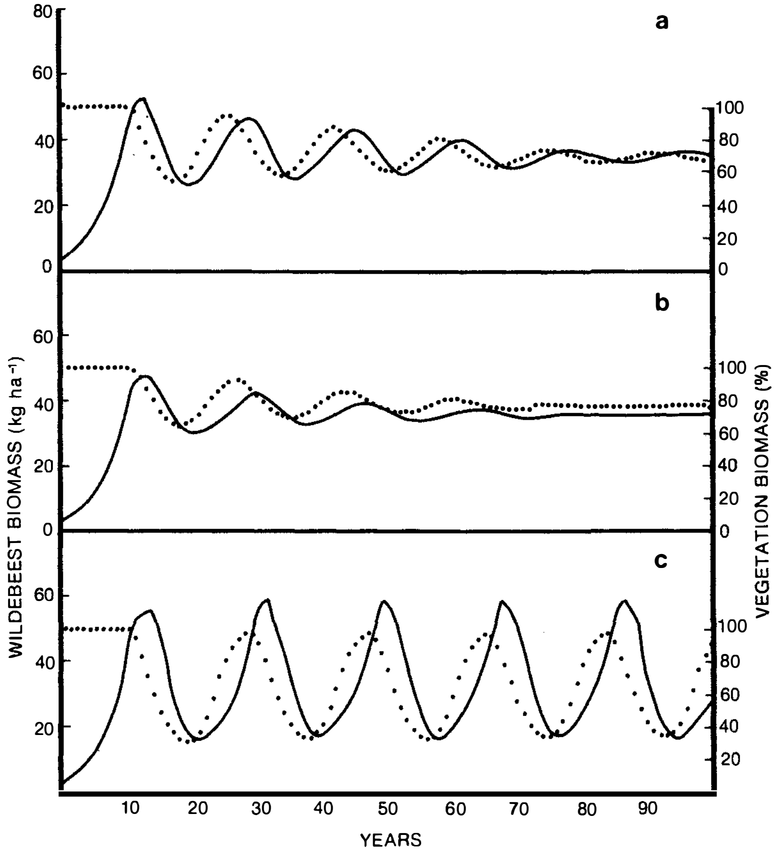

Fig. 13.3 Output from the model showing pattern of increase by a simulated wildebeest population under different conditions. Parameter valued given in Appendix II, rainfall constant, with vegetation interaction. Solid line indicates wildebeest biomass; dots indicate vegetation biomass, as a percent of the maximum. (a) no dispersal, (b) with dispersal, (c) no dispersal, and predation eliminated.

Conclusions for the modelling exercise

The output of the simulation model suggests the following conclusions, which might have some validity for real populations of large herbivores:

1. Population oscillations result mainly from the interaction between herbivores and vegetation, rather than from age structure effects. They develop where levels of consumption by the herbivore at peak biomass are such that plant populations are depressed.
2. Dispersal dampens population oscillations, lowers the peak

biomass level attained, and hence reduces the impact of herbivores on the vegetation. Dispersal also avoids or alleviates the vegetation overutilization that might otherwise develop when drought follows a period of favorable rainfall.

3. Predation and dispersal have basically similar effects on populations. They remove animals before starvation levels are reached, and thereby depress population density below the saturation level set by nutritional limitations. Even if density-independent, and hence strictly not regulatory in their operation, they still have this effect.
4. Smaller ungulates are not intrinsically more or less likely to exhibit populations oscillations than are megaherbivores. This depends on the specific details of their interaction with vegetation, rather than on their demographic characteristics. However, the vulnerability of medium-sized ungulates to predation means that their populations are less likely to reach saturation densities in the absence of dispersal than are megaherbivore populations.

Interactions with vegetation

Is it inevitable that megaherbivore populations increase to densities at which they depress their own food resources, before crashing to a lower density in an impoverished environment, as postulated by Riney (1964)? Megaherbivores – at least elephants, white rhinos and hippos – certainly do modify vegetation structure and species composition, at densities somewhat below their saturation levels. The critical question is, are these vegetation changes detrimental to future food resources?

Jachmann & Bell (1985) present evidence that African elephants respond differently to palatable and unpalatable species of woody plant. Unpalatable species are pushed over independently of their height, while palatable species are pushed over mostly in taller height classes where their canopy is out of reach. Palatable species commonly respond to trunk breakage by coppice regrowth from stumps. The result is the conversion of stands of tall trees offering little accessible forage to dense shrubby regrowth with an abundance of branches within easy foraging reach. Repeated browsing of such patches maintains them in this favorable growth stage for an indefinite period. Examples of woodlands having undergone such beneficial transformations of structure include stands of mixed *Brachystegia* in the Kasungu Park in Malawi (Bell 1981a), and of *Colophospermum mopane* in Luangwa Valley, Zambia. In forest areas elephants of both species encourage, by breaking canopy trees, the growth of gap-colonizing early seral species, which are generally more palatable than slow-growing climax trees (Laws, Parker & Johnstone 1975; Mueller-Dombois 1972).

A further possible benefit is suggested by recent research on plant anti-herbivore chemistry. Repeated heavy browsing of plants may stress them to an extent sufficient to depress their contents of deterrent chemicals (Bryant, Chapin & Klein 1983). By concentrating their browsing on stands of coppice regrowth, elephants may not only make more food available, but also produce better quality food.

Species of *Acacia*, widely favored by African elephants, generally show no seedling establishment under the canopies of mature trees. By pushing over trees, elephants may promote the replacement of mature trees by a much greater density of regenerating saplings, as has happened in the Serengeti (Pellow 1983c). However, other factors such as fire and giraffe browsing can interact to suppress the growth and recruitment to reproductive height classes of these saplings. In many areas feeding by elephants on small plants is sufficient to prevent their recruitment to mature size. Browsing pressure on coppice regrowth of mopane and *Brachystegia* may also be heavy enough to prevent any plants growing through to tree height; but notably mopane at least can produce seed within shrub height classes (R.J. Scholes personal communication). By eliminating baobab, *Commiphora* and other species serving as food sources during drought periods, elephants reduce the ability of future elephant populations to survive droughts. However, if such food sources were not utilized, the population would suffer higher mortality during the current drought.

Under extreme conditions elephants may eliminate woody plants, being forced then to subsist mostly on grass through the dry season. Since dormant grass is a less nutritious food source for elephants than woody browse, the carrying capacity of the habitat for elephants is reduced. The only clear example of such a situation is the Murchison Falls Park in Uganda (although there is suggestive evidence that similar conditions might have been developing in other areas). At Tsavo East in Kenya, woodlands were opened up by the near elimination of *Commiphora* over extensive areas; but other woody species, apart from baobab and *Sterculia*, were less affected, and abundant regeneration of woody scrub has ocurred (Croze, Hillman & Lang 1981).

In the Ruaha Park in Tanzania, elimination of *Commiphora ugogoensis* and depression of *Acacia albida* and baobab populations has not yet exerted any notable effect on elephant population trend. However, a reduced ability of elephants to survive droughts can be anticipated. At Luangwa, the demographic parameters reported by Lewis (1984) suggest that the elephant population has stabilized. While vegetation measurements are lacking, depression of food resources appears limited to destruction of baobabs and local elimination of *Acacia* species (personal observations 1982). Since grasses and mopane shrubbery provide the staple food sources, depression of food availability would seem to be relatively minor.

White rhinos and hippos transform stands of tussock grasses to lawnlike expanses of low-growing or creeping species. Decumbent grasses have a higher leaf to stem ratio, and commonly also higher protein and lower fiber contents in their leaves, than taller grasses. Thus expanses of short grass offer a higher concentration of leaf material and a higher food quality than tall grass stands (McNaughton 1985). However, white rhinos are dependent upon reserves of taller grass for subsistence through the dry season when short grass has been grazed down to stubble. If all areas of tall grass were converted to short grass, white rhinos would become more vulnerable to starvation-induced mortality during drought periods. Trampling by white rhinos furthermore compacts soil structure, and the impact of raindrops on bared soil surfaces also reduces water infiltration. Such effects can lead to reduced grass production from short grass areas.

Hippos at Queen Elizabeth Park in Uganda stabilized during the 1950s at ecological densities three times as high than those attained by white rhinos in the western part of Umfolozi in 1970. Despite such intense grazing pressure, short grass swards persisted, apart from a temporary, drought-related decline. Soil erosion rate increased strikingly, but without worsening effects on food production for hippos (Eltringham 1980; Yoaciel 1981).

Most park populations of elephants are still in a phase of increase from the low densities that persisted at the end of the ivory hunting era at the turn of the century (Spinage 1973). The vegetation structure and composition has developed largely in the absence of elephants over a 70–100 year period. While the state of the vegetation is now being considerably modified by expanding elephant numbers, it is not yet obvious whether long term food production for elephants is being increased or depressed. Only in the Luangwa Valley and Murchison Falls Parks have elephant populations ended their phase of expansion. At Luangwa, the effects on food resources appear minor, at least superficially. At Murchison, the woody browse component was almost eliminated over a large area; but the situation was greatly exacerbated by the compression of elephants into a restricted area by surrounding human settlements.

Caughley (1976b) suggested that the elephant–woodland interaction might generate a stable limit cycle rather than quasi-equilibrium. This outcome seems unlikely, for several reasons. Firstly, even the stability of a limit cycle is unlikely to persist in African savanna environments where rainfall and hence vegetation production vary so widely between years. Secondly, the effects of elephant feeding and related damage on vegetation do not necessarily result in depression of food production. The main effect seems to be a reduction in reserve food sources important during droughts. This could make populations more susceptible to episodic mortality during drought periods. Thus populations may exhibit fluctuations in response to climatic cycles.

Dispersal

For megaherbivores, population stability (in the sense of a dynamic equilibrium with varying food production) can result from lengthened birth intervals and delays in attainment of sexual maturity. However, these population responses are too slow-acting to avert severe vegetation damage and resulting starvation mortality during drought periods. The only adjustment that can prevent or reduce episodic overexploitation of food resources during droughts is dispersal. Caughley & Krebs (1983) suggested that, while dispersal was an important population regulatory mechanism among small mammals, it was unimportant among large mammals. Are megaherbivores thus different from medium-sized ungulates in their dependence upon dispersal?

Among small mammalian herbivores such as voles and hares, there is widespread evidence that populations grow to higher levels, with associated overexploitation of food resources, where dispersal is prevented (Krebs *et al.* 1973). Emigration is an important process in the regulation of snowshoe hare populations, with overutilization of shrubs occurring at peak densities (Keith & Wyndberg 1978; Wolff 1980). Lidicker (1975) distinguished two forms of dispersal among small mammals: (i) presaturation dispersal taking place during the phase of population increase, generally by prime individuals; (ii) saturation dispersal from high density populations, mostly by juveniles and social outcasts. Among small mammals, most dispersal occurs during the presaturation phase, and may be largely density-independent (Gaines & McLenaghan 1980).

Among white rhinos, the territorial system has little influence on dispersal because it affects only a segment of adult males, and not breeding females or immatures. Presaturation dispersal, mainly by subadults, evidently occurs during the phase of population expansion (see Chapter 11). Dispersal movements seem to be partly a direct response to the depletion of habitat resources, and partly an innate tendency to wander during the subadult period. Likewise, African elephants extended their range southwards through the Kruger Park well before they reached saturation densities in the northern district of the park (Pienaar, van Wyk & Fairall 1966b).

Dispersal movements have also been documented for medium-sized ungulates (Owen-Smith 1983). The thar populations studied by Caughley (1970) expanded from nuclei of animals dispersing from the original center of release. Impalas ear-tagged as juveniles in Hluhluwe were subsequently found up to 30 km away in Umfolozi, the initial colonizers being adult males together with immature animals of both sexes (Hitchins & Vincent 1972). For reindeer on South Georgia, signs of overgrazing were followed by the emigration of 400 animals across a glacier that had formerly presented a barrier (Leader-Williams 1980). For white-tailed deer, dispersal rates of 13% per annum were shown by yearling females, and 7% per annum by adult females, with male dispersal rates even higher (Hawkins, Klimstra & Autry 1971). For kudus, in contrast, my own (unpublished) observations indicate dispersal rates of only about 1% per female per year. Dispersal movements certainly occur among most, if not all, ungulates. Rates of dispersal may be lower than they are in small mammals, but so are all other demographic rates.

Small rodents have the potential to more than double their density between years. Thus if mortality and natality rates are functions of the density levels prevailing the previous year, the degree of overshoot of saturation densities will be more extreme than it might be for populations with a lower potential rate of increase. In such circumstances it is advantageous for individuals to move elsewhere, rather than remaining on in a locality where food resources are inadequate to meet demands.

For medium-sized ungulates predation may replace or mask dispersal. Situations of severe resource depletion tend to arise only in circumstances where predator populations have been severely depressed; or where predators are completely absent, as in New Zealand and on other islands.

Megaherbivores are characterized by low mortality and natality rates, and therefore by a high degree of population inertia. They tend to attain biomass levels close to the threshold for vegetation over-exploitation. Furthermore they depress slowly renewing components of the vegetation such as trees or climax grassland. Predation, except in some circumstances by humans in recent times, is a negligible factor for adults. Laws (1969b) stated, with regard to elephant overpopulation, that the important impact of humans in recent times has been to compress populations and block dispersal movements. This conclusion can be generalized to apply to other megaherbivores as well.

Taylor & Taylor (1977) point out that dispersal does not avoid mortality; it merely shifts it elsewhere. Death rates must on average be equal to the sum of *in situ* mortality and net dispersal. Thus emigrants move into areas where their survival chances are reduced relative to source populations. It remains to be explained why dispersal tendencies persist over evolutionary time.

Taylor & Taylor argue that species are confronted repeatedly by hostile situations that are transient and spatially variable in their intensity. Under such conditions, emigrants have a chance of finding more favorable localities, whereas if they remained they would certainly experience starvation induced mortality, or at least lowered reproductive output. Theoretical aspects of this problem have been discussed by Gadgil (1971), Roff (1974, 1975) Lomnicki (1978, 1982) and Taylor (1981a,b). Lomnicki (1978) suggested that population outbreaks are most likely under homogeneous conditions where there are no vacant areas available to absorb emigrants. Hamilton & May (1977) demonstrated theoretically that, even when the mortality of emigrants was extremely high, and the environment offered no vacant sites for colonization, it could still be adaptive for parents to commit more than half of their offspring to be migrants.

Laws (1981a) suggested that in the past elephants experienced a regional mosaic of areas that fluctuated in favorability, with such fluctuations tending to be out of phase in different areas. Nevertheless, the problem remains that long term mortality rates must generally be higher than those measured in local areas in the short term. Thus either emigrants must experience chronically high mortality rates, or catastrophically high mortality must intervene at intervals in established populations.

Major animal die-offs associated with severe droughts are an acknowledged but poorly documented phenomenon. In Botswana, an estimated 15 000 wildebeest died during the 1964 drought, and at least as many again in 1970 (Child 1972). However, the situation was exacerbated by the consequences of the fences erected to control cattle movements, which restricted access to waterholes. In Kenya, the total ungulate biomass on the Athi–Kapiti plains was reduced by 44% during the severe drought of 1961 (Stewart & Zaphiro 1963; Talbot & Talbot 1963b). However, a contributory influence was competition for water with domestic livestock belonging to the Masai people. At Klaserie in the eastern Transvaal, the total biomass of grazing ungulates was reduced to 18% of pre-existing levels by two successive drought years over 1981–83. The main species affected were wildebeest, zebra, buffalo and impala and warthog, with browsers such as giraffe and kudu suffering much less. An exacerbating factor here was the widespread distribution of waterholes, so that no reserve grazing areas remained. In the neighbouring Kruger Park, population declines by susceptible species did not exceed 30–35% (Walker *et al.* 1987).

Population crashes on a similar scale have been documented for elephants at Tsavo East, and for hippos in the Kruger Park. However, elephants and rhinos have survived other equally severe droughts with only minor increases in mortality among the adult segment. The major impact of these droughts falls on juvenile recruitment, both through reduced calf survival and deferred conceptions. It may be that the populations of megaherbivores surviving droughts with little mortality had not yet saturated the carrying capacity of their habitats, so that with time these populations are likely to experience mortality on a similar scale to that recorded for elephants at Tsavo East. On the other hand, there is reason to suspect that the Tsavo East population crash may be an exceptional occurrence, which resulted only because elephants were compressed into a region of very low rainfall by surrounding human disturbance.

Where there are no fence or other restrictions, elephants and white rhinos have responded to food limitations during droughts by wide-scale movements. These may allow animals to locate regions where conditions are somewhat more favorable than elsewhere. Whether this occurs depends on the relation between the scale of spatial variability in the intensity of the drought in relation to the extent of the movements undertaken by the animals. Elephants may move over a distance of 100 km or more, white rhinos over 20 km or more. By such opportunistic movements, animals may escape the full severity of the local conditions reached during drought episodes. Hippos, on the other hand, are somewhat more restricted in their movements; and notably their demographic features tend towards more *r*-selected characteristics than those of other megaherbivores.

As pointed out by Goodman (1981), for large mammalian herbivores comparatively small increases in mortality may have quite a large influence on population trends. Combined with deferred reproduction, regional populations may sag somewhat during drought episodes, then surge back when conditions become more favorable again. However, coupled with the effects of the drought are the impact that populations have on vegetation when animals become forced to subsist on structural components such as large trees or taller grasses. Thus a mosaic effect might result, with the localities that were temporarily more favorable during droughts being severely impacted, then abandoned for a period to recover while the population shifts its centers of concentration elsewhere. In this scenario, fluctuations in regional populations appears as low amplitude, long period ripples, rather than as the more robust ebb and flo experienced by smaller species. However, at the local level plants may experience episodes of extreme concentrations of megaherbivores, followed by recovery periods after centers of animal distribution have shifted elsewhere.

Summary

Megaherbivore populations tend to reach saturation densities at which nutritional limitations restrict further increase. The major regulatory responses occur through changes in fecundity, i.e. in birth intervals and in age at sexual maturity. These may be sufficient to halt population growth without much increase in mortality. Megaherbivores may initiate changes in vegetation structure and composition somewhat below saturation biomass levels. Vegetation changes may result in increased food availability, due to the replacements of mature woodlands or grasslands by faster-growing, more nutritious pioneer plants. However, reserve sources of food used during droughts may be depressed. Dispersal movements allow population densities to adjust in the short term to regional variations on food production related to rainfall variability. Where dispersal is prevented or populations are compressed by human disturbance, local vegetation impact may become severe and precipitate a collapse by the herbivore population. However, in circumstances where large-scale movements can be undertaken, populations may avoid the most severe effects of local droughts, although not without severe impacts on vegetation structure. Regional fluctuations in megaherbivore population levels are likely to be less extreme, and take place over a somewhat longer time scale, than those of smaller ungulates.

14

Body size and ecosystem processes

Introduction

In this chapter I consider how the contribution of large herbivores to community and ecosystem processes varies with increasing body size. The ecosystem features to be covered include the biomass levels sustained, energy fluxes and nutrient cycling through this biomass, and the stability of these features over time. The basic question is, how different would these patterns and processes be if megaherbivores were absent from the system?

Biomass levels

Population biomass

The biomass level that a species population sustains represents a relation between the production of food in the environment, and the ability of animals of the species to transform the food into animal biomass. In African savanna regions, vegetation production is proportional to land surface modified by rainfall, while the resting metabolic requirements of an animal per unit of mass are proportional to its body mass raised to the power minus one-quarter. Therefore, if the amount of food available in the vegetation were independent of body size, the population biomass supported per unit of land area should vary in relation to $M^{0.25}$, i.e. larger species should tend to sustain somewhat higher biomass levels than smaller species.

However, two factors modify the simple relationship developed above. Firstly, the mass-specific metabolic requirements of free-ranging animals, allowing for activity costs, may be scaled in relation to a body mass exponent slightly different from -0.25. For herbivorous mammals, the best available estimate of the scaling exponent is -0.27 (from Nagy 1987, see Chapter 5), i.e. field metabolic requirements scale almost identically to basal metabolic requirements. Secondly, larger herbivores are able to tolerate a lower quality diet than smaller herbivores (see Chapter 5). This means that, for larger animals, a higher proportion of the available herbage becomes acceptable food. Taking into account these considerations, the population biomass levels sustained by large herbivore species should increase with increasing size according to a body mass exponent somewhat greater than 0.27.

Damuth (1981b) examined the relation between local (ecological) population densities and body mass for mammalian primary consumers. For his complete data set, covering some 307 species from mice to elephants, density was related to $M^{-0.75}$. Since biomass equals density multiplied by unit body mass, population biomass levels vary correspondingly in relation to $M^{0.25}$. Damuth also considered relations between density and body mass for local mammalian communities occupying particular habitats in different parts of the world. For none of these communities did the slope of the log–log regression between density and body mass differ significantly from -0.75. Pooling the data from these individual communities yielded an estimate for the power coefficient b relating density to body mass of -0.70 ± 0.08. Damuth concluded that energy metabolism at the population level was independent of body size.

Peters & Wassenberg (1983) examined the relation between abundance and body size for a wider range of animals than was covered by Damuth. For mammalian herbivores of north temperate regions, they obtained a value for the power coefficient b of -0.61 ± 0.14. Thus biomass levels are proportional to $M^{0.39}$. This exponent is somewhat higher than that predicted from the scaling of field metabolic requirements. Peters & Raelson (1984) subsequently found numerical density and body size among mammalian herbivores to be related to $M^{-0.88}$ on a global basis; but the overall slope is biased by the fact that small mammals in North America exhibit densities considerably higher than those shown by small mammals in the tropics. For North American herbivores, ecological density is proportional to $M^{-0.66}$, which is closely similar to the general relation reported earlier by Peters and Wassenberg. However, for 'larger-tropical' herbivores, which includes mainly animals occupying non-forest habitats in Africa and Asia, crude densities are proportional to $M^{-0.30}$, i.e. biomass proportional to $M^{0.70}$. Thus for herbivores in tropical savanna and woodland regions, larger species exhibit somewhat higher biomass levels relative to smaller species than can be explained on the basis of metabolic requirements alone, at least on a regional basis. A similar finding has been reported for local communities of birds, fishes and granivorous rodents (Brown & Maurer 1986). In other words, large species appear to use a disproportionately large share of food resources in these communities.

Herbivore census figures have been published for a number of African national parks and equivalent reserves. However, population estimates are notoriously unreliable, due to limitations in the census methods that can be applied to extensive areas. Aerial surveys tend to undercount small species that are less visible from the air, and are unsuited to woodland habitats and broken terrain. With care, and photographic back-up for large groups, aerial counts can provide reasonably unbiased estimates for populations of species from the size of buffalo upwards. For medium- and small-sized ungulates, aerial surveys need to be supplemented by ground counts, whether by vehicle or on foot, in order to work out correction factors.

Besides the Hluhluwe–Umfolozi Reserve, population estimates for a further ten national parks were selected from the literature as being reasonably unbiased for a range of small to large ungulates. Despite the wide scatter in the population biomasses shown by particular species in different areas, there is a significant positive correlation between biomass and body mass (Fig. 14.1). The weighted linear regression yields an estimate for the power coefficient b of 0.65 ± 0.33, which is close to the value obtained by Peters & Raelson (1984) for larger tropical herbivores. The data for Umfolozi are more reliable than those for any other park, being based on foot estimates from my study areas for smaller species such as duiker and steenbok, and on corrected helicopter counts for larger species.The Umfolozi biomass figures (Table 12.1) yield as estimate for b of 0.76 ± 0.46.

A tendency to undercount smaller species to a greater extent than larger species could be incorporated in even the best census data available, and this effect would tend to bias regression coefficients on the high side. To circumvent this effect, rather than considering regional population totals, one can look at the highest ecological densities reached by each species within local areas of a few square kilometers in extent, preferably estimated from specific studies on the species concerned. For the range of African large herbivores for which such data were obtainable, local population biomass varies in relation to body mass raised to the power 0.71 ± 0.28 (Fig. 14.2). However, most of the variation in local biomass levels occurs among species under 100 kg in body mass. Wildebeest in the Serengeti and waterbuck at Nakuru attain population biomasses of about 9000 kg km^{-2}, closely similar to the maximum biomass levels shown by elephant, hippo, white rhino and buffalo. Black rhino, giraffe and other mainly browsing species exhibit biomasses considerably lower than those of grazers of similar body mass. For grazing ruminants alone, biomass levels appear to increase even more steeply with body mass: for these species, an estimate for b of 1.36 ± 0.50 is obtained.

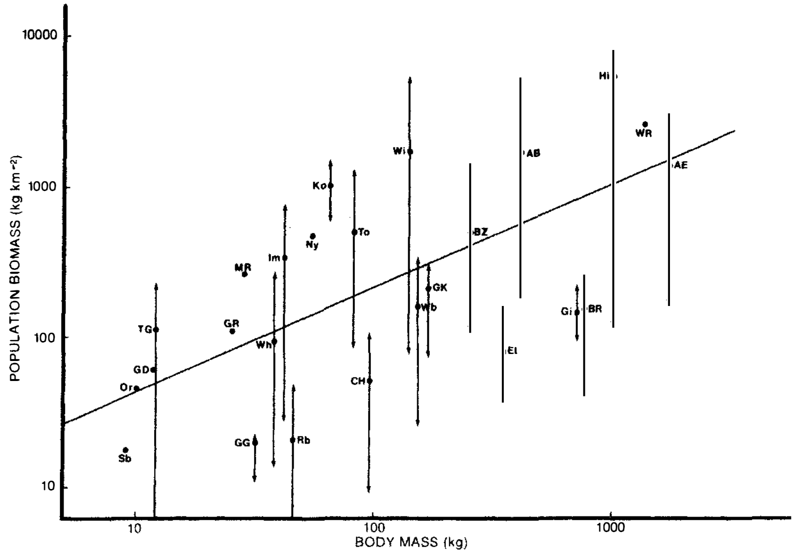

Fig. 14.1 Population biomasses for African large herbivores in relation to body mass. Key to species labels given in Appendix I. Arrows indicate the range, dots the geometric means, for the following National Parks: Amboseli, Kenya (Western 1975); Bouba Njida, Cameroon (Van Lavieren & Esser 1980); Kruger, South Africa (Pienaar 1982); Manyara, Tanzania (Mwalyosi 1977); Nairobi, Kenya (Foster & Coe 1968); Queen Elizabeth, Uganda (Field & Laws 1970; Eltringham & Din 1977); Sengwa, Zimbabwe (Cumming 1975); Serengeti, Tanzania (Sinclair & Norton-Griffiths 1979); Tsavo, Kenya (Leuthold & Leuthold 1976); Umfolozi–Hluhluwe, South Africa (Natal Parks Board unpublished records for 1970 and Table 12.1); Virunga, Zaire (Bourliere 1965). Regression line (based on weighted linear regression): $BIOM\,(\text{kg km}^{-2}) = 6.9\,M^{0.65}$ (SE(b) = 0.016, $R^2 = 0.42$, $N = 113$, $P = < 0.0001$).

Thus for African large herbivores, population biomass levels increase more steeply with body mass than is predicted on the basis of a simple relation between metabolic requirements and body mass. This implies that the effective food density available for consumption increased with increasing body mass, and that over a wide range in body size this increase occurs approximately in relation to $M^{0.70}/M^{0.27} = M^{0.43}$. This means that the abundance of food resources available to white rhino, with a unit body mass of 1350 kg, is over 7 times that available to Thomson's gazelle, with a unit mass of 13 kg. Among grazing ruminants up to wildebeest size, the increase in resource density occurs in almost direct relation to body mass, implying that a 200 kg wildebeest has 20 times as much food available to it as a 10 kg oribi.

Four possible hypotheses may be advanced to explain why large animals

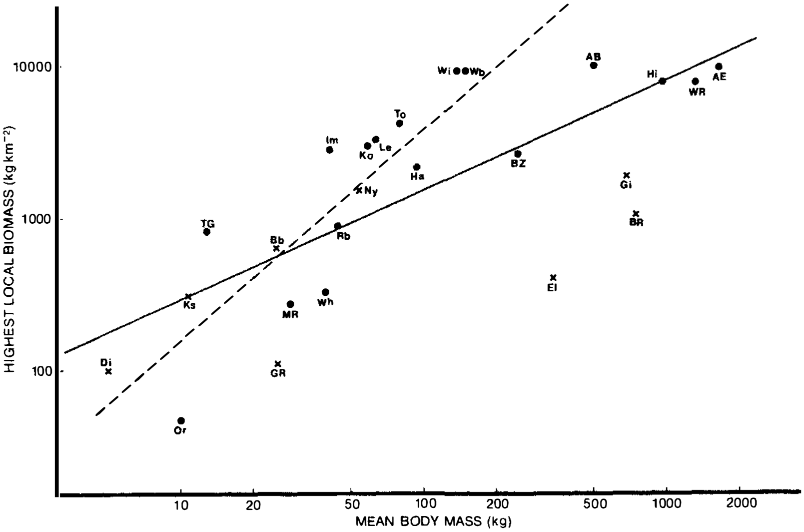

Fig. 14.2 Highest local biomasses reported for African large herbivores in relation to body mass. Dots represent grazers, crosses browsers. Data for each species as follows: African buffalo–Manyara (Mwalyosi 1977); African elephant–Manyara (Douglas-Hamilton 1972); black rhino–Tsavo (Goddard 1970a); bushbuck–Queen Elizabeth (Waser 1974); dikdik–Serengeti (Hendrichs & Hendrichs 1971); eland–Giant's Castle (Scotcher 1982); giraffe–Timbavati (Hirst 1975); greater kudu–Andries Vosloso (Allen-Rowlandson 1980); grey rhebuck–Highmoor (Oliver *et al.* 1978); hartebeest–Nairobi (Gosling 1974); hippopotamus–Virunga (Bourliere 1965); impala–Sengwa (Murray 1980); klipspringer–Semien (Dunbar & Dunbar 1974); kob–Torro (Buechner & Roth 1974); lechwe–Kafue (Sayer & Van Lavieren 1975); mountain reedbuck–Highmoor (Oliver *et al.* 1978); nyala–Lengwe (Bell 1980); oribi–Highmoor (Oliver *et al.* 1978); reedbuck–St Lucia (Venter 1979); sable antelope–Matopos (Grobler 1974); Thomson's gazelle–Ngorongoro (Estes 1967); topi–Queen Elizabeth (Jewell 1972); warthog–Sengwa (Cumming 1975); waterbuck–Nakuru (Wirtz 1981); wildebeest–Serengeti (Sinclair & Norton-Griffiths 1979); white rhino–Umfolozi (this study); zebra–Ngorongoro (Turner & Watson 1964). Regression line (all species); $LBIOM$ (kg km^{-2}) = 56 $M^{0.71}$ (SE(b) = 0.014, R^2 = 0.53, N = 25, P = < 0.0001); for grazing ruminants only (dotted): $LBIOM$ = 9.2 $M^{1.36}$ (SE(b) = 0.26, R^2 = 0.73, N = 12, P = < 0.0004).

utilize a disproportionately large fraction of food resources relative to smaller animals.

1. Large animals can tolerate a lower quality food intake than can smaller animals, as a consequence of the gut capacity–metabolic rate relation (the Jarman–Bell Principle, Chapter 5).
2. Acceptable food patches are more continuously distributed for larger species than for smaller species, with fewer lacunae of unsuitable habitat (Peters & Wassenberg 1983).

3. Being influenced less by predation, larger animals attain densities closer to the saturation capacity of the vegetation than do smaller species (Chapter 13).
4. Larger animals dominate smaller animals in competition for food (Brown & Maurer 1986).

Let me first dispose of the latter two hypotheses. Medium-sized antelopes like wildebeest and waterbuck appear no less susceptible to predation than small antelope like reedbuck and gazelles (see Schaller 1972); yet still achieve a vastly higher metabolic biomass than the latter. Relative invulnerability to predation is a feature only of species in the megaherbivore size range, but biomass levels do not increase significantly between wildebeest size and rhino size.

While interspecific competition between large and small species has been documented for the granivorous rodents studied by Brown *et al.* (1986), it is not a feature of large ungulate communities. Instead the grazing and browsing effects of large species tend more often to increase the availability of herbage that is nutritionally acceptable to small species than the reverse (McNaughton 1976; Chapter 12).

As documented in Chapter 6, large ungulates accept a greater dilution of nutrients by indigestible fiber than small ungulates. This allows them to utilize vegetation components that would be submaintenance in quality for small species, particularly during the dry season period of food restriction; for example the mature dry leaves and stems of grasses, and the roots, bark and twigs of woody plants. There are small mammals with cecalid digestion, including hares and certain rodents, which also consume fibrous plant tissues such as bark and roots, compensating for low nutrient concentrations through increased food intake. Nevertheless, the extent of removal of plant biomass by large herbivores vastly exceeds that documented for small mammals (although not all of the material consumed is digested).

When conditions are favorable, i.e. high soil nutrients relative to rainfall, medium-sized antelope like wildebeest or impala (and domestic cattle) may remove as high a fraction of plant biomass as megaherbivores such as white rhino or hippo. Hence the maximum biomass levels attained for example by wildebeest on the Serengeti Plains are metabolically at least equivalent to the highest biomass levels recorded for megaherbivore species (Fig. 14.2). Below about 100 kg in body mass, ungulates becomes increasingly restricted to the green leaf fraction of the vegetation (Chapter 6).

Very large herbivores furthermore have the ability to utilize vegetation growing in regions of higher rainfall where medium-sized ungulates become restricted in their distribution largely to zones of nutrient concentration, such as floodplains. Although less favorable in terms of nutrient:fiber or secondary metabolite ratios, overall vegetation production in such regions is greater than it is in semi-arid savannas. A notable example is the grasslands of Uganda and Zaire bordering the lakes of the western rift valley, where the biomass is dominated by elephant, hippo and buffalo. However, African elephants are not adapted anatomically to exploit grasses efficiently, while white rhinos at Umfolozi have not been allowed to reach their equilibrium density. An elephant-sized grazer, such as the extinct mammoths or *Elephas recki*, would probably have outperformed any extant species in terms of ability to transform plant biomass into animal biomass.

The extent of the increase in resource use with body size among herbivores in the size range 5–200 kg appears far greater than can be explained by the Jarman–Bell Principle alone. Furthermore, this principle is less applicable to omnivores feeding on seeds and animal matter, which vary relatively little in nutritional quality, than it is to folivorous herbivores. Hence it does not explain the disproportionate use of food resources by large species in communities of birds and rodents, as reported by Brown & Maurer (1986).

On a regional scale, small antelope species like duiker and steenbok appear no less widely distributed than megaherbivores such as elephant and giraffe (for example as shown by species distribution maps for the Kruger Park, Pienaar 1963). However, at the scale of habitat patches as represented by plant communities, steenbok are notably more restricted in their occurrence than are larger browsers like kudu and giraffe (J. T. du Toit in preparation). Thus, large herbivores appear to be habitat generalists, or at least to respond to a larger scale of habitat patchiness, relative to smaller herbivores. This pattern is likely to be typical of other trophic categories besides large herbivores. The patch dispersion hypothesis thus provides the most general explanation for the monopolization of resources by large species at habitat scales equivalent to home range size or larger.

Community biomass

Coe, Cumming & Phillipson (1976) demonstrated a significant relation between the total biomass of the large herbivore community in different African savanna ecosystems and mean annual rainfall. They related this to the controlling influence of rainfall on primary production (Rosenzweig 1968; Rutherford 1980). However, certain areas exhibited a large herbivore biomass about twice as great as that predicted on the basis of the overall mean regression. Coe *et al.* (1976) explained the exceptionally high biomass of large herbivores in the Manyara and Amboseli parks as due to the additional influence of ground water on primary production; and the high biomass in the Virunga and Queen Elizabeth parks to the eutrophic volcanic ash soils prevalent. Notably, however, in all four of the exceptional parks the biomass is dominated by megaherbivores – either elephants or hippos, or both. Umfolozi Game Reserve also exhibits a large herbivore biomass about one third higher than is predicted by the regression derived by Coe *et al.* (1976) for a rainfall of 700 mm (the data for Umfolozi used by Coe *et al.* were derived from earlier, inaccurate censuses by fixed-wing aircraft).

Bell (1982) pointed out that areas underlaid by basement granite were poorly represented in the data set used by Coe *et al.* (1976), and that regions of basement geology exhibit a lower biomass of large herbivores for a given rainfall than areas with volcanic soils or nutrient rich sedimentary deposits. The effect of basement geology is most marked where rainfall exceeds 700 mm per annum, due to leaching effects on soil nutrients. Furthermore, Bell suggests that the predominance of large animals, in particular elephant and buffalo, tends to be higher in savanna regions with basement geology and relatively high rainfall than in nutrient-rich savannas. This effect he related to the tolerance of very large herbivores for the lower quality, more fibrous vegetation that predominates under conditions of low soil nutrient status.

East (1984) divided African large herbivores into two groups depending on how their biomass levels responded to soil nutrient status. Species associated with arid/eutrophic savannas decline in biomass in regions underlaid by basement geology where annual rainfall exceeds about 800 mm; while species associated with moist/dystrophic savannas show biomass levels that increase steadily with rainfall, up to rainfalls about 1000 mm per annum, independently of geological substrate. All megaherbivore species were allied with the arid/eutrophic division of savannas. Elephants in particular showed considerably lower biomass levels, for a given rainfall, in regions underlaid by basement geology than in areas of volcanic material or karroo sediments. However, elephant, hippo and black rhino, together with buffalo and eland, are widely distributed in areas of basement geology with annual rainfalls exceeding 1000 mm; whereas smaller ungulates associated with arid/eutrophic savannas have a restricted occurrence in such regions.

For many African national parks, megaherbivore species together make up from 40% to 70% of the total large herbivore biomass (Fig. 14.3). The exceptions include (i) areas where elephants have been exterminated, or reduced to low numbers, such as Hluhluwe (South Africa), Bouba Njida (Cameroons) and Akagera (Rwanda); (ii) areas of open grassy savanna

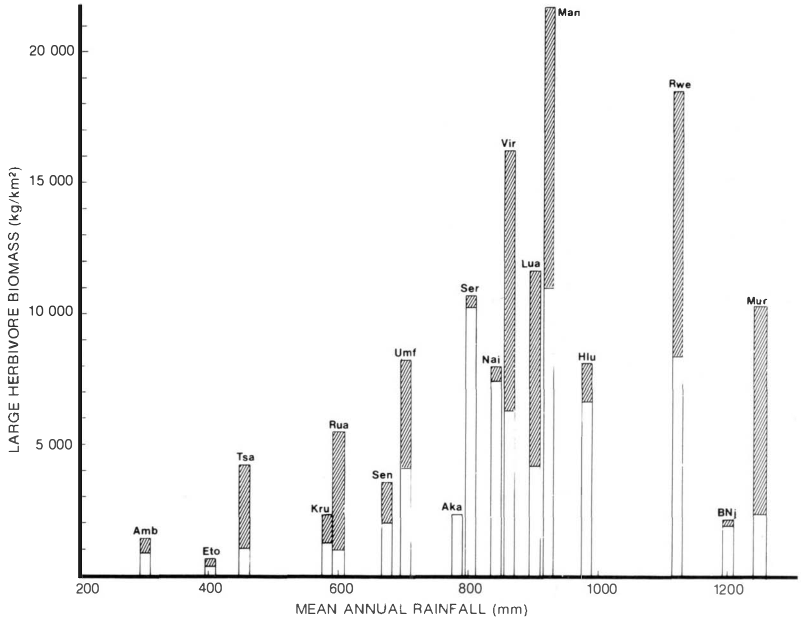

Fig. 14.3 The total biomass of large herbivores in different African ecosystems in relation to rainfall. Shaded segments represent the fraction of the total biomass formed by megaherbivores. Key to species labels given in Appendix I. Based on data reported for the following National Parks: Aka–Akagera, Rwanda (Spinage *et al.* 1972); Amb–Amboseli, Kenya (Western 1975); BNj–Bouba Njida, Cameroon (Van Lavieren & Esser 1980); Eto–Etosha, Namibia (Berry 1980); Kas–Kasungu, Malawi (Bell 1981b); Kru–Kruger, South Africa (Pienaar 1982); Lua–Luangwa, Zambia (Naylor *et al.* 1973); Man–Manyara, Tanzania (Mwalyosi 1977); Mur–Murchison Falls South, Uganda (Laws *et al.* 1975); Nai–Nairobi, Kenya, in 1961 (Foster & Coe 1968); Rua–Ruaha, Tanzania (Barnes & Douglas-Hamilton 1982); Rwe–Rwenzori (Queen Elizabeth), Uganda (Field & Laws 1970; Eltringham & Din 1977); Sen–Sengwa, Zimbabwe (Cumming 1975); Ser–Serengeti, Tanzania (Sinclair & Norton-Griffiths 1979); Tsa–Tsavo, Kenya (Leuthold & Leuthold 1976); Umf–Umfolozi; Hlu–Hluhluwe, South Africa (Table 12.1); Vir–Virunga, Zaire (Bourliere 1965).

where elephants are uncommon, such as Serengeti (Tanzania), and Nairobi (Kenya). In other areas where open grasslands are prevalent, such as Virunga (Zaire) and Rwenzori (Uganda), the abundance of hippos compensates for the moderate densities of elephants; while at Umfolozi white rhinos are the dominant large herbivore.

No relation between the proportion of the total biomass made up by megaherbivores and prevailing rainfall is apparent in Fig. 14.3. The most extreme predominance by megaherbivores occurs in Tsavo (Kenya), under

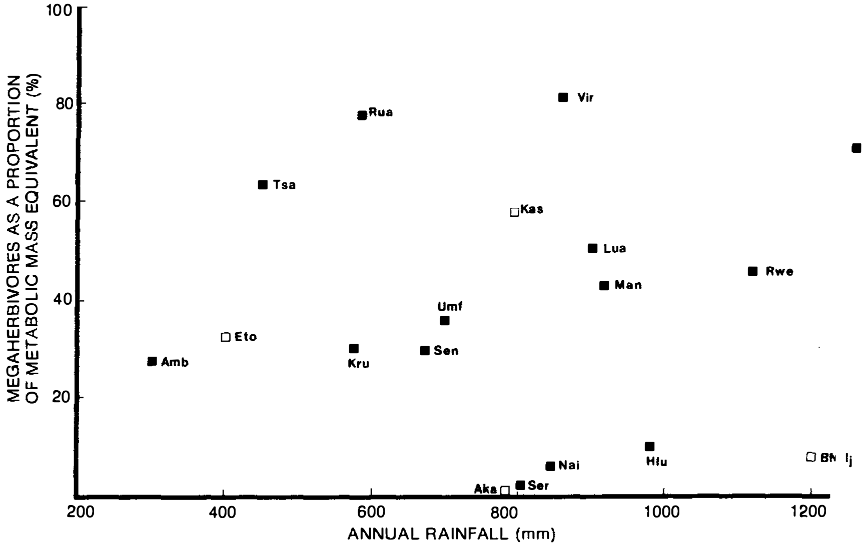

Fig. 14.4 Megaherbivores as a proportion of the metabolic mass equivalent ($M^{0.75}$) of the total large herbivore community in different African ecosystems, in relation to mean annual rainfall. Key to labels and references as in Figure 14.3. Closed symbols represent eutrophic geological substrates, open symbols represent oligotrophic geological substrates.

fairly arid conditions. There are insufficient data for regions of basement substrates to examine the effect of underlying geology on megaherbivore predominance. It appears that megaherbivores of one or more species form the major biomass component in a wide variety of African savanna ecosystems, irrespective of rainfall or geology.

Energy flux

Because of the metabolic weight–body size relation, the fraction that the megaherbivore component contributes to energy turnover by the large herbivore community is somewhat less than is suggested by relative population biomass levels. Proportional contributions to energy turnover may be estimated by transforming body mass into the metabolic mass equivalent, i.e. $M^{0.75}$. On this basis, megaherbivores are responsible for between 30% and 60% of the total energy flux through the large herbivore community for a range of African ecosystems (Fig. 14.4). Exceptions to this pattern are the East African grassy savannas; but this discrepancy may be due simply to the absence of white rhinos, which were formerly abundant in this region, as judged by their prevalence in Pleistocene deposits at Olduvai in Tanzania.

Where megaherbivores are absent, energy flux through the large herbivore component would be reduced correspondingly, unless there were compensatory increases in the density of smaller ungulates. The available evidence suggests that, if compensation occurs, it is only partial. Parks containing megaherbivores exhibit a higher total biomass per unit area of large herbivores than parks under similar rainfall conditions where megaherbivores are absent, or greatly reduced in numbers (Fig. 14.3). The very high elephant biomass at Manyara and Luangwa is not associated with any obvious impoverishment in other ungulate species. In the Mweya Peninsula in Queen Elizabeth Park, a five-fold increase in hippos between 1967 and 1973 was associated with declines by buffalo and elephant; but nevertheless energy flux through the large herbivore community increased to a record 160000 joules h^{-1} km^{-2} in 1973 (Eltringham 1980). In Umfolozi, overall large herbivore biomass and energy flux increased as the white rhino population expanded, until populations were reduced by culling after 1970.

It is widely claimed that ruminant artiodactyls tended to replace cecalid perissodactyls and proboscideans during the course of the Plio-Pleistocene, owing to the superior efficiency of foregut fermentation over hindgut fermentation. This conclusion was challenged by Cifelli (1981) on the basis of the fossil record. The main decline in perissodactyls took place fifty million years ago during the late Eocene, and the radiation of artiodactyls during the Pliocene and Pleistocene was not accompanied by any detectable effect on perissodactyl diversity. In fact periods of increase in generic diversity have tended to coincide in the two orders, suggesting that ruminants and cecalids responded independently to the same environmental factors.

Data for a number of African conservation areas show that cecalids account on average for 35% of the energy metabolism among large herbivores, and that the proportion can be 50% or more in some areas (Fig. 14.5). If *Elephas recki* or white rhino had persisted in many of these faunas, this proportion would be higher still. Thus the amount of energy transformed by hindgut fermentation matches that taking place among the array of foregut fermenters. There is no basis for the contention that hindgut fermentation is less efficient than foregut fermentation, in terms of the primary production metabolized.

The main difference is that ruminants exhibit a much greater diversity of species than cecalids. Typical African ecosystems contain no more than 2–4 species of cecalid, compared with some 12–15 species of ruminant. This contrast in species richness can be explained on the basis of fiber tolerance.

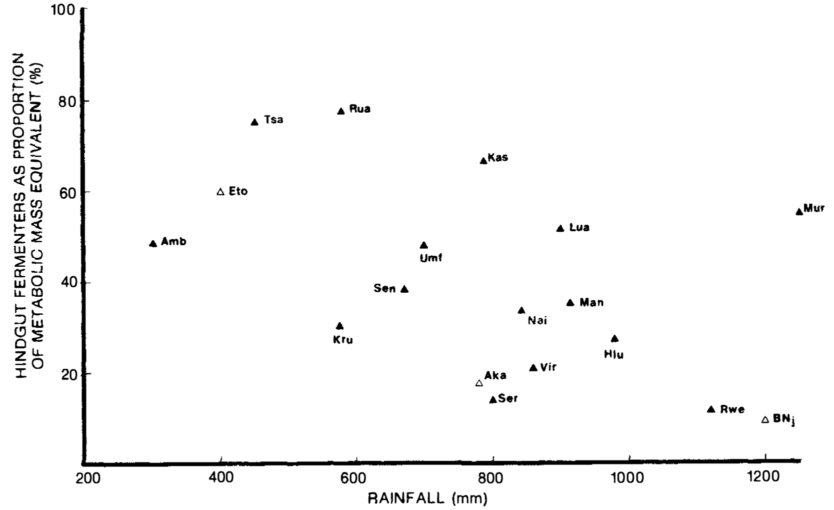

Fig. 14.5 Hindgut fermenters as a proportion of the metabolic mass equivalent ($M^{0.75}$) of the total large herbivore community in different African ecosystems, in relation to mean annual rainfall. Key to labels and references as in Figure 14.3.

Being more fiber-tolerant, cecalid species can exploit a wider range of plant parts and forms than can any one species of ruminant; although, as is typical of ecological generalists, they utilize these somewhat inefficiently. A ruminant species is a specialist for a narrow range of fiber contents, restricted not only by the effects of fiber levels on nutrient concentrations, but also by the consequences for rates of digestive throughput. Bell (1969) noted that zebras have a significantly wider distribution in East Africa than any species of large ruminant, and a similar pattern is evident elsewhere. These relationships have been modelled, and their consequences for niche separation among African ungulates discussed, by Owen-Smith (1985).

The two extant species of elephant are supreme generalists. They consume a spectrum of plant parts from carbohydrate-rich fruits to tall grasses, bark and even the trunks of certain trees. In ecological terms, success is to be measured not in terms of species richness, but rather in terms of the fraction of primary production transformed into animal biomass per unit of land area. Individual species of ruminants may outperform megaherbivores in localized habitats; but if trophic efficiency is assesed within an ecosystem-wide context, African elephants and white rhinos metabolize more plant energy into animal biomass than the most successful species of ruminant, except in extremely eutrophic regions.

Nutrient cycling

Soil nutrient status generally declines with increasing rainfall due to leaching effects. However, Botkin, Mellilo & Wu (1981) presented evidence that, in African savanna ecosystems, soil nutrient status (as assessed by percent base saturation) tends to increase over the annual rainfall range 700–1200 mm, declining at higher rainfall. They related this pattern to the trend shown by large herbivore biomass, which peaks in the range 900–1100 mm annual rainfall. These authors concluded that the large herbivore community makes an important contribution to soil nutrient status by maintaining a pool of nutrients in animal biomass against the forces of leaching. Even though the animal pool is small relative to the nutrient pools in vegetation and soil, its contribution to nutrient cycling is disproportionate, since the turnover rate of animal biomass is vastly greater than that of other pools. Furthermore, nutrients released in faeces and urine are immediately available for quick uptake by plants. In the rainfall range emphasized by Botkin *et al.* (1981), megaherbivores typically contribute 40–80% of the metabolic flux through the large herbivore component (Fig. 14.4). Furthermore, by trampling or pushing over tall grasslands and mature woodlands, megaherbivores accelerate the release of nutrients from these structural tissues via the decomposer chain. By transforming mature phases of vegetation with a slow turnover rate to pioneer phases with more rapid growth rates and higher nutrient concentrations, megaherbivores also increase the amount of acceptable forage available for consumption by smaller ungulates. Changes in soil nutrient status moreover favor faster-growing, more nutrient-rich plant species.

Where herbivore densities are low, the nutrients contained in grass biomass and in tree trunks are released through the agency of fire. However, a large fraction of the nitrogen content is volatilized, while mineral nutrients deposited on the bared soil are susceptible to leaching. By reducing grass biomass, grazing megaherbivores such as white rhino and hippo reduce the incidence of fire. The tendency of woody plants to invade grasslands in the absence of fire may be suppressed by simultaneous browsing pressure from elephant and black rhino.

Jachman & Bell (1985) document the conversion of less productive mature woodlands to more productive stands of shrubby regeneration in the Kasungu Park in Malawi. They propose that this beneficial consequence is effective only in moist dystrophic savannas; and that, even in these savanna forms, increased browse production may fail to materialize where grassy conditions supporting intense fires develop following the opening up of the woodland canopy. In eutrophic savannas, where the woodland is generally dominated by *Acacia* species, open grassy conditions tend to replace savanna woodlands, due to the combined effects of fire and sustained heavy browsing on the regenerating *Acacia* saplings (Bell 1984).

However, in eutrophic savannas most of the grass biomass is of an acceptable quality to be grazed down by white rhinos, and by medium-sized ungulates like wildebeest if they occur in sufficient concentrations. The result could be a herbivore controlled savanna with an open shrubby woody component and predominantly short grass cover, with fire in consequence an insignificant factor. The energy and nutrient fluxes occurring where such conditions prevailed in the past would have been vastly greater than anything recorded in existing ecosystems today, at least where water was not limiting. Nevertheless, there would still have been large areas of Africa far from surface water, where grazing ungulates and elephants would have been sparse, and fire the ultimate non-selective consumer of vegetation biomass.

Ecosystem stability and disturbance

Much of developing ecological theory at the population, community and ecosystem levels has been based on notions that conditions tend towards stasis if undisturbed by human intervention, and thereafter resist further perturbations. However, as the period over which scientists have monitored African savanna ecosystems has been extended (currently up to three decades), stability has become more elusive. The wildebeest population in the Serengeti has increased six-fold, and the buffalo population 2.5-fold, following the elimination of the disease rinderpest from the region. In the Kruger Park, kudu increased 2.5-fold over the decade that I monitored population dynamics, in response to changing rainfall (Owen-Smith 1984). Elephant densities have changed dramatically in a number of parks, due to immigration, poaching or drought. During the 1890s, populations of buffalo, wildebeest and many other ruminants crashed to low levels through most of Africa as the rinderpest pandemic swept across the continent. During the 19th century, elephant and white rhino were reduced to low numbers everywhere, except for elephants in the equatorial forest region, by hunters with firearms.

An alternative ecological perspective, currently taking hold, considers that equilibrium conditions are transient, soon disturbed by events ranging in frequency and scale from fire and rainfall fluctuations to tectonic events and global climatic shifts (Pickett & White 1985; Hansen in preparation).

The pages of this book have revealed little evidence of stasis by megaherbivore populations in recent years. What historic or prehistoric evidence is available further reinforces the picture of disequilibrium and transformation. Archeological evidence from the Tsavo region of Kenya indicates that the vegetation was considerably more open some 100 or more years ago than it was prior to the elephant impact of the 1960s (Thorbahn 1984: Tyrrell 1985). The *Commiphora* shrub steppe prevalent there until recently probably arose following the near elimination of elephants during the ivory hunting era of the 19th century. The dense shrubbery favored tsetse fly, making the region unsuitable for cattle-owning peoples; and it was the lack of a settled human population in the area that led to Tsavo being proclaimed a national park in 1948, rather than any great abundance of animals (Parker 1983).

In recent history, periods of concern about overgrazing by white rhinos, hippos and other ungulates, and damage by elephants to woody plants, have invariably coincided with episodes of below average rainfall (Brooks & Macdonald 1983; Phillipson 1975: Walker & Goodman 1983). Annual vegetation production may decline to 50% of the mean level, and catastrophic mortality among medium-sized ungulates may result if such conditions persist for two consecutive years. Megaherbivores are not immune to large-scale mortality under such conditions, as shown for elephants at Tsavo East and hippos in the northern Kruger Park (Chapter 13). Nevertheless, megaherbivores are more resilient than smaller ungulates to the effects of drought, generally responding by a decline in conceptions rather than by much increase in adult mortality. To subsist through the crisis periods, megaherbivores turn to vegetation components such as woody stems and less nutritious grasslands. The damage that they cause to structural features of vegetation during such episodes of low rainfall may leave a lasting impact on vegetation structure, and drastically alter habitat conditions for a range of other animal and plant species.

In the absence of megaherbivores, fire becomes the major influence on savanna structure. It is this situation that prevailed over much of Africa, especially in the southern part of the continent, until reversed in a few protected parks during the last quarter-century. For the rest of biological time, prior to the invasion by western man and his weapons, megaherbivores were likely to have been a dominant influence on ecosystem structure and dynamics over much of the savanna region of Africa and, as will be shown in the next chapter, the rest of the world.

15

Late Pleistocene extinctions

Introduction

Prior to the late Pleistocene, megaherbivores were represented by a wider variety of taxa than occur today, and were present on all continents. Their disappearance from Europe and the Americas took place at the end of the last glacial period of the Pleistocene, around 11 000 years ago, and was synchronous with the extinction of numerous other large mammal forms. The extinctions occurred during a time of rapid climatic change, with associated transformations in habitat conditions. Another important event took place at about the same time: the entry of humans into the Americas, following their expansion through the furthest corners of the Old World. The relative importance of climate and associated habitat changes versus human predation as causal agents in the late Pleistocene extinctions remains an unresolved problem (Martin & Wright 1967; Remmert 1982; Martin & Klein 1984).

Since climatic change and human range expansion are so closely interwoven in time, wider patterns need to be considered in order to understand the causal links in these extinctions. These include the geographic distribution of extinctions, and variations in the incidence of extinctions among genera of differing body size. In the following analysis I focus specifically on large mammalian herbivores, since it is generally accepted that extinctions of carnivores and of large scavenging birds were related to their dependence upon the herbivores as a food source. It is the herbivores that are likely to be most responsive to changing habitats; and it is also such species that were the prime targets as prey for the expanding human population. By large herbivores, I mean those species weighing more than about 5 kg (the minimum ungulate body mass).

The weight of circumstantial evidence will be evaluated in relation to these questions: (a) Is the climatic shift that occurred around the end of the Pleistocene, and associated habitat changes, a sufficient explanation of the pattern of extinctions among large herbivores? (b) Can human predation alone account for the extinctions? (c) Were both of these factors acting in concert an essential requirement for the extinctions? (d) What were the causal mechanisms leading to the extinctions?

Pattern of extinctions

In North America, terminal dates for extinct species span a narrow range in time between 12 000 and 10 000 years ago. Thirty out of the 40 genera of large herbivores that were reportedly extant during the earlier part of the late Pleistocene (Rancholabrean) disappeared around this time. Extinctions included four genera of megaherbivore: *Mammuthus* (mammoth), *Mammut* (mastodont), *Cuvieronius* (gomphothere) and *Eremotherium* (ground sloth), together with other genera of ground sloths, muskox, deer, camelid and equid. Interestingly, most of the surviving species are from genera that had immigrated into North America from Eurasia earlier in the Pleistocene (Gilbert & Martin 1984; Martin 1984a).

South America suffered an even higher number of extinctions, involving 41 genera of large herbivore. Among these were six genera of megaherbivore: the gomphotheres *Cuvieronius, Haplomastodon* and *Stegomastodon; Toxodon*, a hippo-like notoungulate; and the giant ground sloths *Eremotherium* and *Megatherium.* Also disappearing were genera of equid, camelid, litoptern, edentate and cervid. Terminal dates span a similar time range to those in North America (E. Anderson, 1984; Martin 1984a).

In Europe, six species of megaherbivore belonging to five genera disappeared during the course of the late Pleistocene: *Mammuthus primigenius* (woolly mammoth), *Elephas namadicus* (straight-tusked elephant), *Coelodonta antiquitatis* (woolly rhino), *Dicerorhinus kirchbergensis* (forest rhino), *D. hemitoechus* (steppe rhino) and *Hippopotamus antiquus* (which was somewhat larger than the living *H. amphibius*). Medium-sized ungulates disappearing included the Irish elk *Megaloceros*, the muskox *Ovibos* (which survives in North America), and *Saiga* (which still occurs in temperate Asia). Mastodonts (*Mammut*) became extinct in Europe early in the Pleistocene. *Elephas, Dicerorhinus* and *Hippopotamus* disappeared from continental Europe around the end of the last interglacial some 100 000 years BP, although all of these genera persisted in tropical Asia or Africa. Mammoths existed in Russia until about 11 000 years BP, but disappeared from central and southern Europe somewhat earlier. Dwarf elephants (*Elephas falconeri*) standing only a meter high at the shoulder, and similarly dwarfed hippos, survived in Sicily and other Mediterranean islands until as recently as 8000 years BP. In northern Asia, woolly mammoth and woolly rhino persisted in Sibera until around 11 000 years BP. The giant grazing rhinoceros *Elasmotherium*, bearing a massive single horn on its forehead, survived on the steppes of Manchuria until some time in the late Pleistocene, although precise dates are unavailable (E. Anderson 1984; Davis 1985; Fortelius 1982; Kurtén 1968; Martin 1984a; Vereshchagin & Baryshnikov 1984).

In Australia, a comparable episode of extinctions occurred between 26 000 and 15 000 years BP. This included the rhino-sized *Diprotodon*, giant wombats, and several species of giant kangaroo (Horton 1984).

In southern Africa, three genera of large herbivore disappeared at the end of the Pleistocene between 12 000 and 9500 years ago: the giant buffalo *Pelorovis*, the giant hartebeest *Megalotragus*, and a giant warthog *Metridiochoerus*. Other ungulate species becoming extinct in southern Africa at about the same time included the giant Cape horse *Equus capensis*, and two species of springbok (*Antidorcas*). *Pelorovis* was absent from East Africa after the late Pleistocene, but persisted in the Saharan region until about 4000 years ago. Its extinction from the latter area coincided with advancing desert conditions. An earlier pulse of extinctions occurred between the early and Middle Stone Age periods some time between 200 000 and 130 000 years BP. This included *Elephas recki* (= *iolensis*), *Hippopotamus gorgops, Sivatherium*, the hartebeest genus *Parmularius*, and several large suids (Klein 1984a, 1984b; Martin 1984a).

Further waves of extinction occurred in Madagascar and New Zealand less than 1000 years ago. In Madagascar these included a dwarf hippopotamus as well as giant lemurs and the elephant bird *Aepyornis*. In New Zealand, where mammals were completely lacking apart from bats, extinctions involved particularly the giant herbivorous birds known as moas (Dinornithidae) (A. Anderson 1984; E. Anderson 1984; Martin 1984a).

The wave of extinctions was thus especially severe in both North and South America, involving proportionally about 75% of the genera of large mammalian herbivores on both subcontinents (Fig. 15.1). In Europe and Australia, the episode of extinctions was less severe, accounting for about 45% of large herbivore genera, while the timing of extinctions was somewhat more spread out than in the Americas. In Africa, large herbivore extinctions were minor and no different from earlier pulses during the Pleistocene.

In those continents suffering severe extinctions, the incidence of generic extinction was positively correlated with body size. All megaherbivore genera disappeared, compared with 76% of genera in the size range 100–1000 kg, and 41% of genera between 5 kg and 100 kg. Among small mammalian herbivores weighing less than 5 kg, extinctions involved less than 2% of genera (Fig. 15.2).

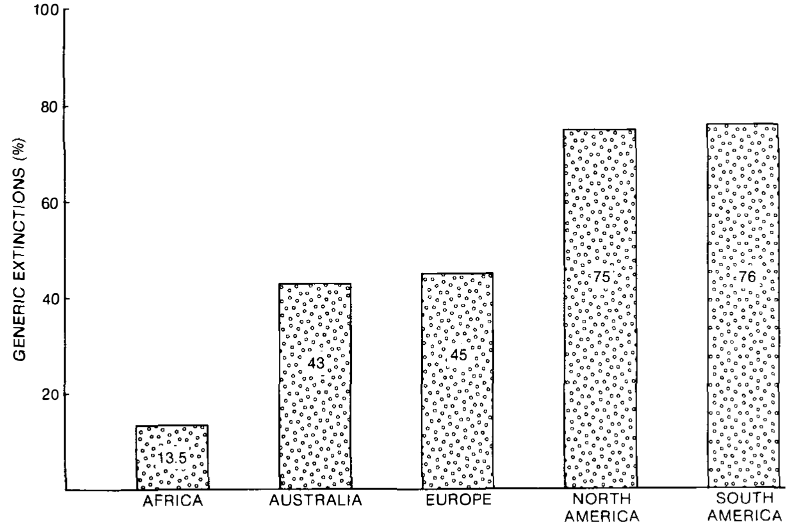

Fig. 15.1 Geographic patterning of late Pleistocene extinctions of mammalian large herbivore genera (this includes all extinctions occurring during the course of the late Pleistocene, i.e. the last 130000 years, of genera with body masses > 5kg). Data from E. Anderson (1984), Klein (1984a, 1984b), Martin (1984a).

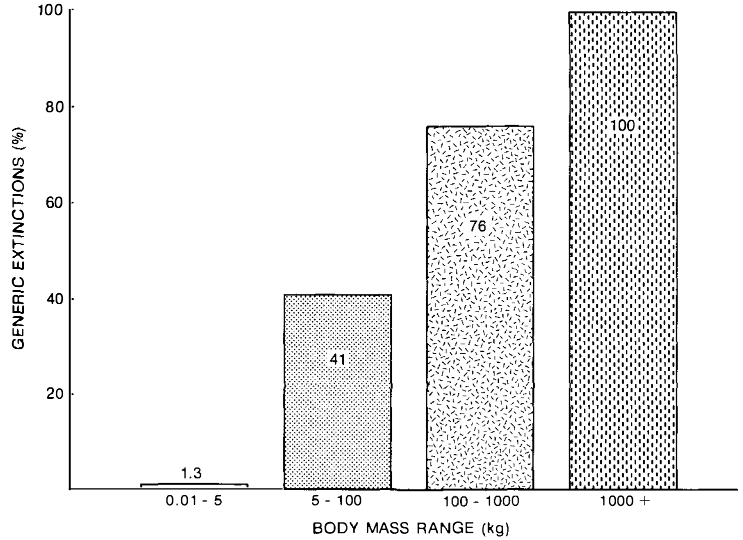

Fig. 15.2 The influence of body size on generic extinctions of mammalian herbivores in North America, South America, Europe and Australia. Sources as in Fig. 15.1.

Climatic change

The paleontological record shows that episodes of extinction commonly coincide with periods of rapid climatic shift. One such period was the end of the Miocene some five million years BP, when global temperatures dropped 5–10 °C and conditions became somewhat drier than they had been earlier (Brain 1985). At about that time more than 60 genera of land mammals (of which 35 weighed more than 5 kg) went extinct in North America, including the last North American rhinoceros (*Teleoceras*) and several genera of gomphothere. Another wave of extinctions occurred around the end of the first glacial cycle of the Pleistocene around two million years ago, when 35 genera of mammal (20 weighing over 5 kg) disappeared from North America. The next major extinction event was that at the end of the Pleistocene, when a total of 43 mammalian genera (39 of which exceeded 5 kg) went extinct. Nevertheless, the total generic richness of the mammalian fauna of North America did not decline until the Holocene, as prior to this time extinctions were balanced by originations and immigrations of new genera (Gingerich 1984; Webb 1984). In Africa, periods of turnover in bovid lineages, including both extinctions and speciations, appear to be associated in time with climatic shifts between wet (pluvial) and dry (interpluvial) periods during the course of the Pleistocene (Vrba 1985).

The habitat changes accompanying the end of the last Ice Age have been documented in some detail for the far north of Eurasia and North America (Hopkins *et al.* 1982). During the glacial period, an open grassy steppe extended from Alaska and north-western Canada through Siberia to northern Europe. The evidence for the grassland rests largely on the associated fauna. Large primarily grazing herbivores predominated, including woolly mammoth, woolly rhino (in Eurasia only), bison, equids, sheep and camelids, together with mixed feeders such as caribou, muskoxen and pronghorn. Other grassland species included badgers, ferrets, ground squirrels and voles. Also present were large carnivores including sabertooths, lions and canids. Browsing ungulates such as moose, elk and smaller deer were rare. How grassy or barren this arctic steppe was is still a source of contention. The pollen record shows only a sparse presence of grasses, together with low shrubs such as *Artemisia* and, in Siberia only, *Selaginella* mosses. Belts of woodland possibly occurred along river valleys. Winter temperatures were frigid, with strong winds redistributing soils in the form of fertile loess deposits. Precipitation was low and probably mainly in summer, so that snow cover was sparse. Winds probably drifted snow into valleys, promoting localized areas of higher plant biomass. Continental glaciers occurred to the east on the Canadian shield, and in the west on the Scandinavian shield.

Global warming began around 14 000 years BP, initiating a rise in sea levels. The Beringian land bridge connecting Alaska to Siberia became submerged, allowing warmer water to penetrate the Arctic Ocean. Winds diminished in intensity as continental glaciers retreated, and more precipitation fell during autumn and winter. The pollen record shows that tree birch (*Betula*) extended its range steadily northwards in North America between 14 000 and 8000 years BP, followed shortly by spruce (*Picea*). The present vegetation in much of Alaska and Siberia is low shrub tundra, with graminoids restricted to waterlogged meadows or stony upland sites. Soils are waterlogged due to underlying permafrost, and leached of nutrients. Large herbivore densities are low, with caribou, muskoxen and moose predominating (Ritchie & Cwyner 1982; Guthrie 1982, 1984; Hopkins 1982; Matthews 1982; Schweger 1982).

The environmental changes that occurred in the far north were extreme, involving a radical transformation of the entire ecosystem – climate, soils, vegetation and fauna. It is difficult to imagine a grazing ungulate fauna surviving in the habitats occupying this region today. Mountain sheep remain in mountainous areas, and bison persist to the south; but mammoth, woolly rhino, equids, camelids and antilocaprids have vanished.

In the conterminous United States, the mid-continental grasslands and southern deserts date only from the early Holocene. During the last (Wisconsin) glacial, the prevailing vegetation over much of the continent was a coniferous parkland or open forest, with an admixture of hardwoods and an understorey of shrubs, grasses and forbs. This parkland occurred south of the steppe-tundra in a broad band from the east coast to Wyoming and as far south as Georgia and Kansas. Open herbaceous vegetation similar to the modern prairie occupied southern Illinois until 35 000 years BP. Wetter conditions than those of today prevailed in the region of the Great Salt Lake in Utah. Communities of animals and plants were generally more diverse than they are at present. For example, in the Appalachian region mammoth, mastodont, ground sloths, bison, equids, muskoxen, caribou, stag-moose (*Cervalces*), deer and tapir coexisted during the late Pleistocene.

The border between steppe and forest vegetation shifted steadily northwards as conditions warmed at the end of the Pleistocene, reaching northern Minnesota about 11 000 years BP and Quebec about 10 000 years BP. In South America, the most pronounced change was a large-scale contraction of open steppe habitats about 10 000 years BP, with forests thereafter becoming much more extensive (Gilbert & Martin 1984; Guilday 1984; Markgraf 1985; Wright 1977, 1984)

In Europe, open steppe vegetation extended through the British Isles and into northern France during the height of the last (Weichselian) glaciation. During this period, around 20 000 years ago, mammoth, bison, horse and reindeer were abundant in France, as documented in cave paintings. To the south of the herbaceous steppe, a shrub steppe graded into forest composed of spruce, pine, larch, birch and alder. As the climate warmed, shrubs extended northwards, with tree birch reaching Denmark and Poland about 12 500 years BP. By 11 000 years BP, a birch–poplar–pine forest covered most of north-western Europe, although the forest was open and parklike on its northern fringe. Areas of open larch parkland still persist today in places in Siberia (Wright 1977; Yurtsev 1982).

In Australia, hyperarid conditions expanded over most of the continent between 26 000 and 15 000 years BP. During this period, woodlands became restricted to a narrow band along the east coast (Hope 1984; Horton 1984).

In Africa, the Pleistocene was characterized by alternating wetter and drier conditions. Drier conditions favored a predominance of grazing ungulates, and wetter ones a predominance of browsers. A mainly grazing ungulate fauna prevailed in the Cape between 30 000 and 12 000 years BP, since which time browsing ungulates have predominated. At a site in the northern Transvaal where the local vegetation is currently mixed deciduous savanna, vegetation over the past 35 000 years varied between an open forb-rich grassland with forest patches, and semi-arid Kalahari thornveld. At one time in the late Pleistocene, open country grazers like blesbok and springbok extended their ranges into Zimbabwe where *Brachystegia* woodlands now prevail; while at other times lechwe, a grazer of seasonally flooded grasslands, occurred in the southern Kalahari region. On the East African plateau, conditions were drier than at present during the latter part of the last glacial period and open grassy vegetation was prevalent. At the beginning of the Holocene, there was an expansion of forests, although not sufficient to displace the grassy savanna on most of the plateau (Klein 1984b; Livingstone 1975; Scott 1984; Vrba 1985).

The habitat changes that occurred at the end of the Pleistocene involved more than just latitudinal shifts in vegetation biomes. Species of plant and animal responded individually to environmental changes, so that the ecological communities we find today are very different from those existing during the Pleistocene. Graham & Lundelius (1984) proposed that 'coevolutionary disequilibrium' between plants and herbivores was a factor in the extinctions. Guthrie (1984) suggested that the mosaic interspersion of communities that prevailed during the Pleistocene was transformed into a broader scale zonation of vegetation in the Holocene, and that the resulting decline in local habitat diversity made it more difficult for large herbivores to secure their seasonal habitat requirements.

However, to account for the late Pleistocene extinctions, evidence is needed that the climatic and habitat changes between the last glacial period and the Holocene were more extreme in rate or magnitude than was the case during the numerous previous transitions between glacial and interglacial conditions. Guthrie (1984) proposed that there is a trend of intensifying seasonality, reaching greater extremes during the Holocene than during previous glacial or interglacial periods. The evidence for this is drawn largely from the differences in faunal community structure between the Pleistocene and the Holocene. Species that today exist only in the central and southern United States coexisted in Pleistocene faunal assemblages alongside species now occurring only in the far north of Alaska and Canada. Some evidence of increasing resource restrictions comes from the decline in body size shown by many lineages, including mammoths, towards the end of the Pleistocene. However, the record of temperature changes, as indexed by oxygen isotope ratios both in marine foraminifera and in Antarctic ice, shows no significant difference in rate between the Illinois–Sangamon and Wisconsin–Holocene transitions. Furthermore, during the Sangamon interglacial temperatures evidently rose to 2–3 °C warmer than those experienced during Recent times (Shackleton *et al.* 1983; Lorius *et al.* 1985). Hence the reorganization of habitats relative to glacial conditions was likely to have been more extreme then than at present.

The extreme habitat transformations that occurred in the far north are sufficient to account for the extinctions of grazing ungulates in this region. However, the almost synchronous disappearance of a variety of large herbivore genera at lower latitudes in North America, and from tropical as well as temperate South America, remains unexplained. All of these lineages had survived numerous previous transitions between glacial and interglacial conditions, albeit as new species or with evolutionary modifications. In Europe, grazers, including horse, ass, camel, yak and saiga, survived on the steppes of central Asia; only megaherbivores and muskox disappeared. Extinctions were equally severe in both North and South America; while in Africa and tropical Asia, at similar latitudes to South America, extinctions were few.

No explanations have been advanced as to why habitat changes were especially inimical to the survival of megaherbivores. As was documented in previous chapters, extant elephants and rhinos are tolerant of a wide variety of food sources and habitat conditions. During the Pleistocene, woolly mammoth had an enormous geographic range, extending through Eurasia from Spain, Italy and China in the south to Russia and Siberia, and in North America from Alaska to the Great Lakes region. Further south it was replaced by the Columbian mammoth, which extended from the United States through Mexico as far south as El Salvador. Judging from their fossil remains, mammoths of various species were especially abundant over most of this range throughout the Pleistocene. Woolly rhino were prominent in Pleistocene faunas through much of Eurasia, especially in Mongolia where grassy steppe still persists (Agenbroad 1984; Vereshchagin & Baryshnikov 1984).

From what is known about the ecology of extant species, the following kinds of habitat changes would have been especially detrimental for Pleistocene large herbivores: (i) reduced habitat diversity, particularly a lack of adjacent food resources for both the periods of summer growth and reproduction, and winter subsistence; (ii) a marked lowering of soil nutrient status, and hence of forage quality both of grasses and woody browse; (iii) a general reduction in the standing biomass of available food, or of its accessibility, due for example to a persistent cover of deep or crusted snow. Nevertheless, it is difficult to understand why the Holocene grasslands of the United States and Central Asia were inadequate for the continued existence of such tolerant grazers as mammoths must have been. Even the most uniform regions of vegetation have local zones of higher diversity along rivers or alluvial fans or in mountainous areas. Bison persisted in vast numbers on the mid-continental grasslands; while the Columbian mammoth, which had been abundant throughout this region during the Pleistocene, fell by the wayside. Extinctions included not only grazers, but also browsing mastodont and gomphothere, and semidesert inhabitants such as some of the ground sloths and camelids.

While there are numerous examples of megaherbivore extinctions prior to human presence, these were generally associated with ecological replacements. For example, in Europe mastodonts were replaced by *Elephas namadicus*, which was likewise a woodland browser. In contrast, the late Pleistocene extinctions involved the termination of particular ecological types in the fauna.

Thus hypotheses based on climatic change fail to explain either the geographic distribution of extinctions, or the fact that likelihood of extinction increased with body size among herbivores. Extinctions in the Americas and Europe coincided in time with a period of rapid climatic and habitat change, but in Australia they were associated with a period of climatic extreme. There is no independent evidence, apart from biotic changes, to show that the climatic change between the last glacial period and the Holocene was more extreme than during previous glacial/interglacial transitions. However, reductions in body size indicate that many herbivore species were under nutritional stress, and distributional changes of species suggest that seasonality may be more extreme today than it was in the past.

Human predation

In Europe, humans gradually extended their range northwards during the late Pleistocene, reaching 50 °N latitude by about 40 000 years BP. The earliest evidence of human hunting of mammoths dates from around 70 000 years BP. Specialized hunting of mammoths is associated with narrow flint speartips capable of penetrating the thick hide. Human interest in the Pleistocene megafauna, including mammoth, rhino, bison and reindeer, is graphically illustrated in cave paintings in France dating from about 20 000 years BP. Mammoths are absent from fossil assemblages after about this time in south-western Europe, southern Russia and China; while other species formerly associated with mammoths in steppe faunas, including horse, bison and reindeer, persisted. In Russia and Siberia, there is abundant evidence of humans hunting mammoths, horses, bison and reindeer, and in some places woolly rhinos. Some encampments in Siberia have houses constructed from the accumulation of mammoth bones. The most recent European dates for mammoth, from the Ukraine and Switzerland, are from around 12 000–13 000 years BP. At the end of the paleolithic period between 12 000 and 10 000 years BP, *Mammuthus primigenius, Coelodonta antiquitatis* and *Ovibos* disappeared finally from their last refuges in Siberia (Liu & Li 1984; Martin 1982; Müller-Beck 1982; Vereshchagin 1967; Vershchagin & Baryshnikov 1984).

In North America, the earliest unequivocal evidence of human occupation dates from around 13 000 years BP. Claims for earlier human presence are based on rather dubious artefacts and remain controversial, especially in comparison with the cultural stage reached by source populations in Eurasia by that time. At about 11 500 years BP, the characteristic stone spear-heads of the Clovis culture became abundant throughout the conterminous United States. After 11 000 years BP, the Clovis points were abruptly replaced by the somewhat different stone points of the Folsom culture. While Clovis points commonly accompany mammoth remains, Folsom points are associated only with bison and smaller species. There is also evidence of the hunting of mastodonts during Clovis times. In the conterminous United States, the most precise terminal dates for extinct species, from Racholabrea, California, cluster between 11 200 and 10 800 years BP, i.e. at the end of the Clovis period. The disappearance of ground sloths from the Grand Canyon in Arizona occurred close to 11 000 years BP. Elsewhere, the youngest reliable dates for mammoth, mastodont, ground sloth, equid, camelid and stag-moose are around 10 500 years BP. In Alaska, last dated records of mammoth are around 13 500 years BP (Fisher 1984; Haynes 1982; Marcus & Berger 1984; Mead & Meltzer 1984; Phillips 1984; West 1984).

In South America, there is evidence both of human presence and of the hunting of gomphotheres in Venezuela from at least 13 000 years BP, and from Brazil perhaps as far back as 32 000 years BP. Humans had evidently reached southern Patagonia by 12 600 years BP. By about 11 800 years BP gomphotheres had disappeared in Venezuela, although other now extinct species persisted until about 10 000 years BP. In Patagonia, ground sloths were not recorded after 10 500 years BP. Records elsewhere suggest that some of the extinct forms may have persisted until as recently as 9000 years BP (Gruhn & Bryan 1984; Guidon & Delibrias 1986; Markgraf 1985; Martin 1984a).

In Australia, the entry of aboriginal people from south-east Asia occurred prior to 30 000 years BP, and humans had spread as far south as Tasmania by 25 000 years BP. However, associations between human artefacts and large vertebrate fossils are rare. The main wave of large mammal extinctions occurred around 18 000 years BP, the coldest period of the last glacial, with a few species persisting at the southern fringe until 15 000 years BP (Horton 1984; Murray 1984; Reed 1970).

In Madagascar, there is close coincidence between the arrival of the first human occupants around 1000 years BP, and the disappearance of such large animals as dwarfed hippopotamus, several genera of lemurs, two species of giant tortoise, and two genera of giant flightless birds. In New Zealand, the extinction of moas followed closely in time the arrival there of the Maori immigrants from Polynesia. Evidence of human hunting of moas is plentiful (A. Anderson 1984; Martin 1984a; Trotter & McCulloch 1984).

Hominid presence in Africa has been continuous and continent-wide since the time of the Pliocene australopithecines. *Homo erectus* spread from Africa to tropical Asia in the mid-Pleistocene perhaps 700 000 years ago. Both these regions have thus had a long association between the evolving human lineage and the large mammal fauna. The Middle Stone Age people occupying southern Africa between 130 000 and 70 000 years ago hunted mainly eland and other medium-sized ungulates, and evidently avoided elephants and rhinos. Late Stone Age people occupying this region after 40 000 years BP hunted especially warthogs and bushpigs. Human predation may have been a factor in the extinctions of giant buffalo and giant hartebeest at the end of the Pleistocene (Klein 1977, 1984a, 1984b; Volman 1984).

Martin (1967, 1973, 1984a and b) has been the chief protagonist for human overkill as the prime cause of the large vertebrate extinctions of the late Pleistocene. Support for this hypothesis rests on the disproportionate extinctions among larger mammals relative to other animal groups, particularly in the Americas where animal populations would have been especially vulnerable through lack of previous contact with humans. The close synchrony between the appearance of humans and animal extinctions at different latitudes in Europe lends further support. Recent extinctions of large mammals and birds in Madagascar and New Zealand are unequivocally related to human colonization of these islands. However, in Australia the aboriginal colonists coexisted with the megafauna for some 10 000 years before the main wave of extinctions occurred.

Martin (1984b) envisaged a 'blizkrieg wave' of humans spreading southwards through the Americas. Vulnerable animal species were quickly eliminated, forcing the colonists to keep moving on. This unsettled pattern is advanced to explain the paucity of associations between human cultural artefacts and the extinct fauna in North America, in contrast with the situation in Eurasia. Martin claims further support for this hypothesis from the close synchrony between the terminal dates for large mammal species in particular regions, and the putative time of arrival of human hunters, as they dispersed southwards.

The frequent associations between mammoth remains and Clovis spearpoints indicates that human predation on mammoths was relatively common. However, dates for mammoth fossils in North America do not support Martin's notion of a blitzkrieg wave rolling southwards (Agenbroad 1984). A further challenge comes from reported dates of human presence and hunting of large mammals in South America predating the Clovis period in North America.

However, the main problems confronting the overkill hypothesis are (i) to explain the synchronous disappearance not only of mammoths, mastodonts and ground sloths, but also of a wide range of medium-sized mammals, many of which are not obvious prey species for humans; and (ii) to account for the extinctions of certain species of bird, and of some small mammal species, that were not directly dependent upon the large mammal fauna for prey or carrion (Grayson 1977; Stedman & Martin 1984).

The role of megaherbivores

Human predation was undoubtedly a major factor in the extinctions of megaherbivores. There is abundant evidence of the importance of mammoth, and to a lesser extent woolly rhino, as a prey of humans in northern Eurasia. There is also clear evidence of human hunting of mammoths, mastodonts and gomphotheres in the New World shortly before their disappearance. The responses that modern elephants and white rhinos adopt against carnivores is to stand ground, protecting young animals behind the bodies of adults. However, such tactics are inappropriate against an organized band of humans armed with projectile weapons. Very large animals that had evolved with no contact with humans would be especially vulnerable to this novel predator. Even after aeons of coevolution, white rhinos still vacillate between standing their ground and fleeing when confronted by humans approaching from upwind. In contrast, African elephants and black rhinos react aggressively to any close approach by humans, in a way sufficient to inhibit hunting by humans not armed with guns. In Africa and tropical Asia, large mammals were able to improve their defenses as humans gradually improved their skills as hunters. In northern Europe, the confrontation was more sudden as humans spread northwards. In the Americas, it was particularly cataclysmal, as hunters who had perfected their techniques over centuries of practice in northern Eurasia met a particularly naive fauna.

The extinction of *Elephas recki* in Africa between the Early and Middle Stone Age periods cannot readily be ascribed to human predation, since archeological sites show that African hunters of the time avoided very large mammals. Nevertheless, indirect effects of human hunting may have played a part. The developing reliance of humans over this period on hunting larger animals rather than scavenging probably entailed increased control over fire as a tool in attracting animals and removing screening vegetation. From its grazing dentition, *E. recki* would have been dependent more on grass and less on woody browse than the modern *Loxodonta africana.* Thus regular removal of the tall grass cover by burning would have been especially detrimental to its subsistence through the dry season.

Burning is, however, beneficial to a short grass grazer like the white rhino, able to feed in the green flush following the fire. The disappearance of white rhino from East African savannas early in the Holocene could well be related to increasing hunting skills by humans occupying this region. White rhinos persisted into modern times only in the southern and north-central regions of Africa. The former area was occupied only by stone age hunters until perhaps 2000 years ago; and among the Iron Age colonists, the Zulus at least did not regard white rhino meat as edible. The latter area remained relatively uninhabited even in the present century.

For a predator to drive its prey to extinction, there are just two requirements: (i) a rate of harvest exceeding the maximum sustained recruitment rate of the prey population; (ii) the possibility for predation to be sustained even when prey become rare. For modern megaherbivores, maximum rates of population increase vary from 6–7% for elephants to about 10% for hippos. If mortality due to predation were to exceed such levels, populations would decline inexorably towards extinction. A possible scenario is (i) a regional prey density of about 2 per km^2; (ii) a regional human density of 0.05 per km^2 (similar to that estimated for the European paleolithic); (iii) a kill rate of one animal per band of 25 people per week sustained over the year.

Megaherbivore populations under nutritional stress due to adverse habitat changes would be less able to sustain the harvest quotas reported above. Populations restricted to localized pockets of acceptable habitat by the climatic reorganization of the terminal Pleistocene would have been especially vulnerable to being hunted down to the last animal; in particular, animals as large as megaherbivores have nowhere to hide. But what about the smaller ungulates, with higher potential rates of population increase, that also went extinct? For them a human overkill scenario is far more difficult to sustain.

We must turn next to a consideration of the consequences of the elimination of megaherbivores from ecosystems. Prior to human arrival, populations of mammoths, mastodont and ground sloth would have existed at saturation levels where further increase was prevented by food limitations. Vegetation would undoubtedly have been in a severely disturbed state. Grazers such as *Mammuthus, Stegomastodon* and *Mylodon* would have consumed or uprooted a large fraction of grass biomass, creating areas for colonization by low-growing pioneer grasses. In such disturbed grasslands, fires would have been less severe, allowing establishment by woody trees and shrubs. However, these large beasts may have prevented the woody component from growing into a mature woodland by incidental behaviors such as rubbing or exercising strength. Browsers such as *Mammut, Cuvieronius, Haplomastodon, Megalotherium* and *Eremotherium* would have created open gaps by felling trees in more heavily wooded habitats. These gaps would have been colonized by faster-growing, and hence more palatable, species of tree and shrub. A better-developed herb layer in these gaps may have allowed fires to penetrate, promoting further opening of the tree canopy. Such activities by both grazing and browsing megaherbivores acting in concert would have produced the kinds of savanna parklands, with a diverse mixture of different species of tree and herb, as have been identified from the pollen record. From this perspective, the change to less diverse zonal vegetation at the end of the Pleistocene would not be a causal factor in the megaherbivore extinctions, but rather a consequence of the removal of their disturbing influence on plant communities.

What would the consequences of these habitat changes have been for smaller herbivores? Such species had coexisted with megaherbivores through all of their evolutionary time. The kinds of vegetation changes that megaherbivores induced would have been beneficial in terms of stimulating growth by the more nutritious pioneer species of grass and shrub, and by creating a small-scale mosaic of plant communities. Furthermore, the activities of megaherbivores would have facilitated nutrient cycling, leading to further improvements in nutritional quality. Many of the medium-sized ungulates may have been dependent over a large part of their range on the kinds of habitats created by the presence of associated species of megaherbivore.

With the demise of mammoths, mastodonts and giant ground sloths, forests would have tended to close in, and taller grasses to expand so as to support fierce fires. The distributions of smaller species of herbivore must have contracted to localized sites of edaphic disturbance where a diversity of more nutritious species of plant still persisted. Discontinuities in the distribution of suitable habitat following the removal of megaherbivore disturbance may have made it more difficult for these species to follow shifting vegetation zones through the climatic changes of the late Pleistocene. Whether these habitat changes alone were sufficient to cause the extinctions of other species of herbivore, or whether human predation on the localized and vulnerable populations was necessary, must remain conjectural.

In summary, the scenario that I propose follows this sequence:

1. Sustained human predation causes naive populations of megaherbivores to decline as harvests exceed replacement potentials.
2. The climatic and habitat changes associated with global warming compress megaherbivore distributions and places these species under increased food stress, making them more vulnerable to being hunted to extinction.
3. The disturbing influence of megaherbivores on vegetation is thereby removed, leading to trends towards dominance by late successional plant species and more uniform zonal habitats.

4. Vegetation becomes less favorable for smaller herbivores, inducing population declines by these species, with predation by humans deprived of megaherbivores probably promoting their slide towards extinction; a crucial factor was perhaps the inability of the island population remnants to follow shifting vegetation zones.
5. Mammalian carnivores and scavenging birds decline due to the disappearance of much of their food resource.
6. Birds and other small vertebrate species dependent upon the disturbed habitats created by megaherbivores disappear.

It has been frequently claimed that climatic change was the major factor leading to the extinctions of large herbivores in the late Pleistocene, with human predation a secondary factor placing additional stress on populations. My conclusion is that extinctions were inevitable for those megaherbivore species with a maximum rate of population increase inadequate to support sustained human predation. The timing of the extinctions may have been controlled largely by habitat change, which confined populations to localized areas, thereby making them more vulnerable to sustained human hunting until the last pair had been killed. Thus the hyperarid period of the late Pleistocene in Australia may have made populations of *Diprotodon* and giant kangaroos such as *Sthenurus* especially sensitive to being hunted to extinction by the early Aborigines.

Whatever the interwoven effects of habitat change and human predation were in the late Pleistocene extinctions, there are certain basic points to be emphasized. The one certain factor distinguishing the terminal Pleistocene from the end of the previous glacial periods was the presence of humans as sophisticated hunters. Human hunting must inevitably have had a great impact on the populations of very large species, which had been largely free of predation by carnivores except on juveniles. The elimination of the impact of megaherbivores must inevitably have caused habitat changes, apart from those brought about by climatic shift. By hunting to extinction the vulnerable herbivores, humans initiated habitat transformations that may have played an important role in the extinctions of lesser herbivores, apart from their direct hunting impact on these species. In other words, if it had not been for human presence, most of these species would have survived into the Holocene. Thus I conclude that human predation on megaherbivores was the necessary and sufficient cause of the wider spread of extinctions among large mammals at the end of the Pleistocene.

Summary

The disappearance of numerous genera of large mammals and birds at the end of the Pleistocene has been related both to the major climatic and habitat changes occurring at this time, and to human overkill. Neither explanation is adequate in isolation. Climatic hypotheses fail to explain the geographic concentration of extinctions in the New World, and the positive correlation between extinctions of mammalian herbivores and large body size. Human predation readily explains the elimination of megaherbivores, but not of numerous smaller species.

The demise of megaherbivore populations through their inability to sustain organized human predation resulted in the removal of their positive influence on vegetation diversity and nutritional content. This precipitated cascading effects on other species dependent upon disturbed habitats. Human predation on megaherbivores was thus the prime factor in the late Pleistocene extinctions, with the climatic changes and their effects on vegetation aiding the timing of the extinctions.

16

Conservation

Introduction

The decline of megaherbivores did not end with the termination of the Pleistocene. During the nineteenth century, expanding human settlements and continued hunting reduced Asian species to isolated populations, and ivory exploitation led to African elephant becoming rare over most of southern, eastern and western Africa. Following the advent of firearms, white rhino declined in southern Africa from a widespread and abundant species to the brink of extinction over the course of 60 years. In north-east Africa, white rhino recently suffered an even more dramatic decrease, from several thousand animals distributed through three countries in the early 1960s, to a remnant of about 15 restricted to one park in Zaire at the time of writing. Over much of Africa, remaining populations of elephant and black rhino are suffering steady attrition due to continuing human exploitation for ivory and horn. Javan rhino and Sumatran rhino were listed by the IUCN among the world's twelve most threatened animal species; Indian rhino, Asian elephant and black rhino are listed as endangered; and African elephant and white rhino, while currently safe numerically, remain vulnerable to poaching pressures.

Where populations of megaherbivores have been effectively protected, a contrasting conservation problem has arisen. Populations have increased to levels where they have induced vegetation changes such as to threaten the survival of other animal and plant species in these areas. As a result elephant, hippo and white rhino have been culled in the sanctuaries set aside for their protection. Besides these three species, the only other ungulate that has been culled routinely in a large national park (one of over 2000 km^2) is buffalo (in Kruger and Hwange). Cumming (1982) pointed out that, apart from elephant and hippo, no large herbivore species has been responsible for major vegetation degradation unrelated to human interference through actions such as provision of artificial water supplies, predator reduction or confinement to relatively small areas.

The choice of action to combat or alleviate both of these problems continues to generate much argument among conservationists. Is intervention in the form of culling really necessary in order to safeguard habitat conditions for other species? Should megaherbivore populations be exploited for economic gain? Can rapidly diminishing populations be effectively protected in the wild, given the limited extent of most conservation areas? Is the effort in terms of finance and manpower required to protect these species justified? Much of the debate revolves around philosophical differences in attitudes and objectives among conservationists. Thus I will first outline the various objectives of conservation. From this perspective, I will assess the merits and likely consequences of different actions, making recommendations for the most effective choices of action in relation to problems both of overabundance and of overexploitation.

Conservation objectives

In terms of the 'World Conservation Strategy' formulated by the International Union for the Conservation of Nature and Natural Resources (IUCN), the objectives of conservation are (i) to sustain life support processes; (ii) to maintain biotic diversity; (iii) to retain those species, or ecosystems, of particular benefit or interest; (iv) to keep future options open (IUCN 1980; Miller 1983). In the context of national parks and other designated conservation areas, these broad objectives tend to get translated into the more practical goal of retaining the full historic diversity of habitats and species in the region (Leopold *et al.* 1963; Leopold 1968; Brooks & Macdonald 1983; Pienaar 1983).

Conflicting with this goal is the fact that habitats and populations are not static. Thus the question becomes, how much change is permissible? Walker & Goodman (1983) suggest that preventing change causes ecosystems to lose resilience. This means that their biotic communities become less capable of absorbing climatic stresses or other disturbances, which inevitably occur sooner or later, resulting in more severe losses of species than would otherwise have occurred. There is increasing awareness among ecologists that disturbances of varying severity, frequency and extent (including fire, drought, floods, hurricanes, disease, and climatic shifts) have been an integral component of ecosystem functioning in the past. Observations both on coral reefs and in tropical forests suggest that species diversity is highest at intermediate levels of disturbance (Connell 1978).

Another conservation viewpoint places emphasis on conserving a representative suite of natural ecosystems, to serve as benchmarks against which to compare adjoining man-modified regions. This may involve the establishment of so-called biosphere reserves, encompassing conservation areas as integral units alongside adjoining developed areas. For national parks to function as benchmark ecosystems in this context, natural processes must be allowed to proceed with minimal human intervention. Nevertheless, the effects of surrounding developments, for example the ingress of alien species, may intrude into parks and require combatting (Caughley 1981; Ferrar 1983; Houston 1971; Siegfried & Davies 1982; Sinclair 1983).

More pragmatic concerns relate to the cost-effectiveness of conservation. If the future existence of national parks is to be safeguarded in developing African countries, they should not be a financial drain on the limited economic resources of these countries. Their persistence would be more secure if they generated material benefits for these countries, and more particularly for surrounding rural people. From this perspective, controlled hunting of species like elephants and rhinos, together with the sale of animal products like ivory, could make a particularly valuable economic contribution (Anderson 1983; Konigkramer 1983; Martin & Taylor 1983; Myers 1972).

Problems of overabundance

Elephants

African elephants have been responsible for changes in vegetation in a number of conservation areas, as outlined in Chapter 12. Such changes are generally regarded as threatening to the continued survival of the plant species damaged, and of habitat conditions for other animal species, as well as detrimental to aesthetic qualities of landscapes. Nevertheless, reductions in species diversity as a result of elephant-induced changes in vegetation are undocumented. Declines in certain tree or animal species have undoubtedly occurred; but whether these decreases were balanced by increases in other formerly rare species remains uncertain. Reports from Tsavo in Kenya suggest that, while woodland ungulates declined following the elimination of *Commiphora* thickets by elephants, open country grazers increased (Parker 1983).

In Kruger Park in South Africa and Hwange Park in Zimbabwe, elephants have been culled routinely to contain their populations within pre-assigned limits, with the aim of restricting vegetation changes. In other parks in Namibia, Zimbabwe and Uganda, temporary cropping operations have been carried out to reduce elephant populations. A cropping operation was also started at Luangwa Valley in Zambia, but abandoned due to its inefficiency. In Kenya and Tanzania, intervention in the form of culling has been resisted, except for a few limited operations for scientific purposes. Extensive habitat changes have occurred in some parks where laissez-faire management was followed, for example at Tsavo in Kenya and Ruaha in Tanzania. However, vegetation changes perceived as detrimental have not been avoided in parks where culling has been carried out.

Barnes (1983a) analyzed the factors involved in deciding whether to initiate elephant culling in the Ruaha Park in Tanzania, with the aim of halting the rapid and progressive decline in certain tree species in the rift valley section. To not only stop the woodland decline, but also allow the potential for recovery, about three-quarters of the total population of 24 000 elephants would need to be removed. The logistics of such an operation lay beyond the capabilities of the Tanzanian wildlife department. The most cost-effective time for culling to be initiated would have been before woodland damage became notable.

In the Nuanetsi region of Gonarezhou Park in Zimbabwe, a reduction of the elephant production by 40% (from 2 per km^2 to 1.3 per km^2), combined with culling of impala, resulted in vastly improved regeneration by *Acacia* trees in the riverine fringe. However, a 20% reduction of elephants in the Chizarira Game Reserve, also in Zimbabwe, alleviated woodland damage for only one year. In the Kruger National Park, where pre-emptive culling is carried out to prevent elephants from increasing above a ceiling density of about 0.4 per km^2, between 300 and 700 elephants are removed annually. Ivory, hides and meat resulting from this operation are marketed at a considerable profit. However, this policy did not prevent severe damage to tree populations from occurring during the 1982–84 drought. Furthermore, concern has been expressed about the cruelty to the elephants and the disturbance of their behavior resulting from chasing by helicopter and killing by paralysing drugs (de Vos *et al.* 1983).

White rhino and hippo

White rhino and hippo exert their modifying impact on the grass layer. The result is not only changed grassland conditions for other animals, but also increased soil erosion. Accelerated rates of sheet and gully erosion threaten the overall productivity and stability of the ecosystem. Soil is a slowly renewing resource, so that losses cannot be remedied in a short time span. Furthermore, with fires precluded, grassland areas tended to become invaded by *Acacia* scrub. These are the classical symptoms of the 'overgrazing' problem that is widespread in areas of human subsistence pastoralism over much of Africa.

In the Umfolozi Reserve, the management response to the grassland changes brought about by expanding populations of white rhino and other grazing ungulates was to institute culling programs aimed at reducing the densities of these species. The target densities were based on agricultural assessments of permissible stocking densities for cattle in the region. The white rhino population was reduced from 1550 in 1970 to 1070 in 1976 and 600 in 1982. All rhinos were caught and removed live, animals being transported to other wildlife areas, or sold to private farms and zoos. The wildebeest population was reduced by about one third over this period, with other ungulate species affected somewhat less. Overall a 50% reduction in large herbivore biomass was achieved between 1972 and 1983. As a consequence, very little increase in animal mortality occurred during the severe drought experienced over 1982–83. Following exceptionally high cyclonic rainfall in early 1984, grass recovery was striking not only in the culled area, but also in a control block left unculled (Brooks & Macdonald 1983; Owen-Smith 1973, 1981; Walker *et al.* 1987).

Hippos at high densities cause similar changes in grasslands and soils, although only a 3 km wide zone adjoining rivers or lakeshores is affected. To arrest the perceived habitat deterioration, seven thousand hippos were removed from the Queen Elizabeth National Park in Uganda between 1957 and 1967, the meat being made available to local people. Another four thousand hippos were cropped in the Murchison Falls Park. After cropping ended, hippos regained their former densities; but the grassland remained in an improved condition, perhaps due to higher rainfall (Eltringham 1980; Laws, 1968b, 1981b).

General problems

In general terms, managers are concerned about the following consequences of the vegetation changes induced by expanding megaherbivore populations: (i) radical modification of certain habitat types, leading perhaps to the loss of species dependent upon them; (ii) elimination of certain sensitive plant species; (iii) reduced vegetation cover leading to accelerated erosion and a decline in the overall productivity of the ecosystem; (iv) depression of the resource base for megaherbivore populations themselves; (v) loss of aesthetic features of landscapes, such as mature trees or lush grasslands.

As outlined in Chapters 13 and 14, vegetation changes are inevitable as megaherbivore populations increase towards saturation levels at which they become limited directly by food resources. At the time that national parks and game reserves were established, the prevailing vegetation communities had developed under low megaherbivore densities, due to past hunting. To some degree, vegetation is now merely reverting to its state in prehistoric times, when megaherbivore populations were unaffected by human hunting. Nevertheless, the rate and extent of vegetation change may be greatly exacerbated where animal populations are compressed into the confines of national parks by surrounding human disturbance.

The term 'overabundance' used in the heading to this section is a value judgement, implying that populations exceeding certain levels are detrimental to the objectives of conservation. However, some level of vegetation disturbance is probably beneficial to both habitat diversity and productivity. The vegetation impact of megaherbivores is only likely to become detrimental if it exceeds the disturbance regimes that prevailed over the evolutionary times of associated species, in either magnitude or frequency (Hansen & Owen-Smith in preparation). However, there is no *a priori* basis for specifying what these prehistoric regimes were. The only way to discover what they might have been is to create conditions as close as possible to those prevailing before intervention by modern man.

In Chapter 13, I argued that dispersal was the major short term process adjusting megaherbivore populations to the changing carrying capacity of their habitats. As a result of the suppression of dispersal movements by fences, settlements, hunting and other boundary restrictions, megaherbivore densities are likely to be higher and less responsive to rainfall-related variations in vegetation growth than would have been the case in the evolutionary past. The impact of elephants on trees, and white rhinos or hippos on grasses, may hence reach such extreme severities, and persist for sufficiently extended periods, as to lead to lowered species diversity. Sensitive tree species, like baobab, may be virtually exterminated, except in inaccessible localities such as steep hillslopes. If reserve grazing in the form of tall grass stands are eliminated, populations of white rhinos and other grazers become vulnerable to large-scale population crashes during droughts, with increased risks of local species extinctions during such events (Owen-Smith 1983). Hence laissez-faire inaction cannot be justified where ecological processes have been distorted by boundary restrictions. Some form of population manipulation is needed to counteract the effects of fences or other inhibitions on movements.

Population culling as currently applied has generally been aimed at achieving some arbitrarily set population level. For example, the target elephant density in the Kruger Park simply represents one elephant per square mile, a figure originally suggested on the basis of the elephant densities that were believed to exist in both the Kruger and Hwange National Parks at the time that problems of vegetation damage were first confronted. Subsequently, more accurate counts showed that the elephant density in Hwange at the time was about 2.5 times this figure. At Luangwa Valley in Zambia, the elephant density reached was three times that in Hwange, although rainfall was only 40% higher (poaching has subsequently reduced this density). The relatively low density of elephants maintained in Kruger Park has not prevented severe damage to certain tree species and woodland types. In the Serengeti, damage to mature *Acacia* woodland occurred at an elephant density of under 0.2 per km^2.

Similar considerations apply to short grass grazers such as white rhino and hippo. Even at low densities, white rhinos concentrate their grazing in existing short grass patches, and by removing the grass cover accelerate soil erosion from these areas. At higher densities, larger areas become affected. The choice as to the most desirable ratio of short grass to tall grass grassland is debateable.

Somewhat different concerns arise from the effects of culling operations on behavior and population structure. Adverse behavioral responses to humans, whether in vehicles or on foot, can degrade the experience of visitors to parks. In the Kruger Park, elephant culling is organized so as to take out complete family units, the aim being to minimize the disturbing effect on the rest of the population. Nevertheless, the mean distance travelled over a 12 hour period by surviving family units in clans from which other family units had been culled was 19.2 km, compared with 6.1 km for undisturbed family units (Hall-Martin, quoted by de Vos *et al.* 1983). The long range communication among elephants at sound frequencies below the audible range of humans could provide a means for transmitting panic responses through the population. Despite supposedly random selection procedures, buffalo culling in the Kruger Park is strongly biased towards subgroups of non-breeding individuals within herds (Mason & van der Walt 1984). Disruption of population structures reduces the potential for future scientific studies. Furthermore, pre-emptive culling may also pre-empt the operation of the processes of natural selection that have shaped the characteristics of the species.

Dispersal sinks

The conditions prevailing in national parks and other conservation areas today differ in one major respect from the situation in prehistoric times: the presence of boundaries restricting dispersal. Even if park boundaries are not fenced, movements beyond borders are generally inhibited by settlement and hunting in the surrounding area. Parks in effect tend to become island ecosystems, at least so far as larger mammals are concerned, and thus become subject to the kinds of changes that island communities experience. Populations of some species tend towards higher densities than they would attain under conditions where free dispersal was possible, while other populations become vulnerable to extinction. If the area is too small, the genetic diversity of populations may decline through inbreeding (East 1981; Lomolino 1985; Soule 1980).

If national parks and similar conservation areas are to replicate the conditions that prevailed within their borders in pristine times, opportunities for dispersal need to be created to reduce the island effect. Where emigration is prevented or inhibited by boundary fences or adjoining human disturbance, dispersal sinks must be created within the borders of the conserved area. This can be done by designating certain areas as vacuum zones for particular species. Culling would be carried out periodically so as to remove all animals of that particular species settling within the vacuum zone. No culling would be carried out in the remainder of the park, where populations would be allowed to attain their own equilibria, buffered from extreme change by the dispersal option allowed by nearby vacuum zones (Owen-Smith 1974a, 1981, 1983; Petrides 1974).

Vacuum zone culling offers these potential advantages:

1. The surplus individuals to be culled are selected by natural mechanisms operating within the population.
2. Population densities in the rest of the area can adjust to the supply rates of food resources, and the fluctuations therein associated with rainfall variations.
3. There is no artificial distortion of population structure within the bulk of the population.
4. Aesthetic qualities in the remainder of the park remain untarnished by the side-effects of culling operations.
5. Spatial diversity is enhanced. In particular the vacuum zones serve as refuges for those species sensitive to the impact of megaherbivores on vegetation.

Several practical issues arise with regard to the implementation of vacuum zone culling. I answer each of these in turn.

1. Will rates of dispersal be adequate to halt population increase before vegetation damage is incurred? The answer to this is clearly no. Vegetation damage in the form of tree breakage, or suppression of tall grasses, occurs even at low densities of elephants or white rhinos. The term damage is moreover a subjective one. It should be rephrased as damage to conservation objectives, i.e. detriment to overall species diversity. From this perspective, if dispersal is unimpeded then species diversity must be closely similar to that which would have occurred in prehistoric times. The vacuum zones

ensure the retention of vulnerable species – for example baobabs in the case of elephant, or reedbuck in the case of white rhino.

2. Will animals not become conditioned to avoid vacuum areas as a result of the culling carried out in them? Elephants are well known to be sensitive to hunting disturbances. For example, in the Luangwa Valley where controlled hunting areas adjoin the national park, elephants cross the river into the hunting areas in the evening and move back into the security of the park at dawn (Lewis 1986). If culling were carried out regularly in the vacuum zones, this would inhibit their colonization. The solution is to ensure that culling is carried out irregularly in the form of brief blitzes. Thus animals within the vacuum zones are killed or captured before they have a chance to react to the culling operation. After such an operation, any animals remaining in the region would be left unmolested for a time sufficient for any fear responses to fade, due to lack of reinforcement.

3. Would not the large number of animals removed from vacuum zones in a short period saturate marketing outlets? This is an inherent problem with reduction cropping operations. However, the number of animals to be removed from any one vacuum zone would not be large – at the most, perhaps 100 elephants or white rhinos – and culling can be rotated among different vacuum zones. Moreover, since population densities within the vacuum zones are kept well below saturation levels, there is no special time urgency in scheduling: culling can be carried out when it is most convenient in terms of markets, manpower and facilities. The culling team, whether part of the wildlife department or a private contractor, could move from one vacuum zone to another according to a pre-arranged and planned schedule. Operations could furthermore be carried out with maximal efficiency, since there is no need for concern about the age or sex classes of social units to be removed.

4. How many vacuum areas would be needed, and how large would each need to be? Vacuum zones need to be distributed so that they are readily encountered by animals moving out of saturated zones. They should be selected initially to be somewhat smaller than the home ranges covered by population units, so as to avoid depleting neighboring populations.

For example, for white rhinos in the Umfolozi-Hluhluwe complex, I recommended that four vacuum zones be established, each covering about 50 km^2 (Owen–Smith 1973). The total area encompassed by the vacuum zones would thus represent 20% of the total conservation area. Vacuum zones situated around the periphery of the reserve would facilitate the removal of animals with least blemish to the rest of the reserve. Where feasible, it would be an even better arrangement for vacuum zones to be located in adjoining tribal areas, so that harvesting could be carried out by neighboring people to their direct financial benefit.

In the case of white rhinos, demographic adjustments in the population core caused by nutritional limitations could halve the annual rate of increase from nearly 10%, as prevailed at the time of my study, to about 5%. With a total population of 1500 white rhinos in the 750 km^2 of core area, about 75 animals would need to be removed annually. However, the number to be removed from each vacuum zone would not be a constant figure; it would vary in relation to conditions of food availability within the core area, which in turn will vary in relation to rainfall. There would be no need to calculate any quota. The procedure would simply be to remove all the white rhinos found within the limits of the vacuum zones about once every four years.

In the case of African elephants, each vacuum zone would need to cover 250–500 km^2, the approximate extent of clan home ranges. Since elephants have a slower rate of population increase than white rhinos, each vacuum zone could be culled only about once every 10 years. This low frequency of culling would probably be adequate to avoid conditioning elephants against entering the vacuum areas.

5. Should the siting of vacuum zones be rotated? It would be preferable to retain vacuum zones in fixed locations. This allows a contrast in habitat conditions between these zones and the rest of the conservation area to build up, with beneficial consequences for overall spatial heterogeneity and species diversity. Vacuum zones thus become permanent fixtures sited most conveniently for removals. It is unlikely that habitat conditions would become so extreme as to discourage immigrants, at least during crucial drought periods.

6. Is vacuum zone culling applicable to ungulates besides megaherbivores? Intervention in the form of culling is necessary only for those species that (i) can exert a major impact on habitats, and (ii) for which natural population regulatory mechanisms are too slow-acting to alleviate such impacts. For ungulates from the size of buffalo downwards, predation can act to depress populations below the level at which vegetation impact becomes severe and persistent. Though there can be time lags before predator populations respond to prey increases, $r_{\max}$ values are higher for carnivores than they are for ungulates (Western 1979). Thus I consider that culling is justified for smaller ungulates only where predator populations are artifically depressed – as they are in many small conservation areas. However, vacuum zone culling would hardly be practical in such small parks, though this depends on the home range extent of the species causing problems in relation to the size of the area.

Problems of overexploitation

At the time of writing, problems of megaherbivore overabundance persist only in South Africa, Zimbabwe, Botswana and Namibia. Elsewhere in Africa, situations of perceived overabundance of elephants have been transformed within a few years into problems of rapidly dwindling populations. Rhino populations have undergone particularly rapid attrition throughout the continent north of the Zambezi. The cause is organized illicit hunting, spurred by the vastly inflated prices fetched by rhino horn and ivory.

Such patterns demonstrate dramatically the sensitivity of megaherbivore populations to human predation. The maximum population growth rates that can be sustained by such large animals are slow: a harvest of 10% in the case of rhinos, and 7% in the case of elephants, would be sufficient to push populations into steady decline. In a moderate-sized national park containing say a thousand rhinos or elephants, a rate of loss to poaching of 6–8 animals a month would initiate a downward plunge in numbers that would accelerate over time. Outside of equatorial forests, these huge beasts can find no seclusion from determined hunters.

Megaherbivore populations can sustain only a very limited degree of human exploitation for subsistence or profit. The elephant culling routinely undertaken in the Kruger Park in South Africa, and at Hwange in Zimbabwe, has been commercially viable in the absence, until recently, of any losses to poachers in these areas. Unless the control of such illegal hunting is very tight, the population surplus left for any legitimate economic exploitation can easily be reduced to zero. Moreover, modelling demonstrates that the economically most profitable time to harvest elephants for ivory is upon their death from old age, due to the fact that tusk growth continues throughout life (Pilgram & Western 1986). This would not apply to rhinos, from which horns can be removed without killing animals. However, proposals to remove horns from rhinos on a commercial basis would make minimal contribution to the conservation of these species, except in the form of a few mutilated specimens in certain small parks.

Effective responses to situations of overexploitation lie firmly within the socio-political realm. The need is to restrict rates of harvest to the low levels that populations can sustain; and the only way to achieve this effectively where the products are highly valuable is to have exceptionally tight control over marketing. There must be no illicit avenues through which products such as horns or ivory can be moved. This shifts the conservation focus into the international economic realm of customs regulations, embargos and cartels, and other factors impinging on the values and uses of animal products. If control as strict as this cannot be achieved, megaherbivore populations must drift inevitably downwards in the direction of extinction (Martin & Martin 1982; Parker & Amin 1983).

Summary

Megaherbivores pose two contrasting problems for conservationists, (i) overabundance associated with vegetation destruction; (ii) dwindling numbers due to illicit exploitation. Problems of elephant overabundance have been widespread in Africa, resulting in a severe impact on certain woody plant species. Hippos in Uganda, and white rhinos in Umfolozi, have attained biomass levels associated with elimination of tall grass cover and soil erosion. Vegetation disturbance need not be detrimental to ecosystem productivity or species diversity; but where dispersal is restricted or prevented, populations may remain at high biomass levels long enough for critical thresholds for recovery to be surpassed. By creating dispersal sinks within conservation areas, such risks could be reduced, with minimal interference with natural population processes in the remainder of the conservation area.

With regard to dwindling populations, the problem is that human hunting can easily exceed the maximum replacement rate. Populations may be reduced to low numbers within a short period, as has happened with elephants and rhinos through most of Africa. Without effective control of illicit markets, populations of these great beasts will be driven inexorably towards extinction.

17

Epilogue: the megaherbivore syndrome

In the preceding chapters of this book I have documented a variety of aspects of the ecology of those large mammalian herbivores that exceed 1000 kg in adult body mass. I have analyzed how these ecological features are related to the allometric trends evident among smaller species of large herbivore. I have pointed out a number of phenomena that appear to be characteristic of these so-called megaherbivores. I now want to draw together these threads to assess the degree to which megaherbivores share in common a distinct set of coadapted features, which can be referred to as the megaherbivore syndrome.

Faunal patterns

Only in parts of Africa and tropical Asia are the faunal communities of today representative of those that prevailed during the Pleistocene and earlier times in the geological record. In Africa the five extant species of megaherbivore make up only a small fraction of the total species diversity of large (> 5 kg) herbivores present continent-wide. The distribution of some 79 herbivore species in different ranges of body size suggests the existence of three modes in species richness: (1) at a body size of about 100–200 kg, made up largely of ruminant artiodactyls occupying savanna habitats; (2) at a body size of about 20 kg, consisting predominantly of forest duikers; (3) a small outlying blip in the megaherbivore size range, with most of these species being non-ruminants (Fig. 17.1).

In terms of animal biomass distribution, a contrasting pattern emerges. The major peak lies in the megaherbivore size range, with the secondary peak formed by medium-sized ruminants (Fig. 17.2). However, in terms of relative energy turnover, as indexed by $M^{0.75}$, the two peaks are closely equivalent. Thus in terms of ecological efficiency, as measured by the fraction of primary production metabolized through the herbivore trophic level, one adaptive mode is formed by the diversity of medium-sized

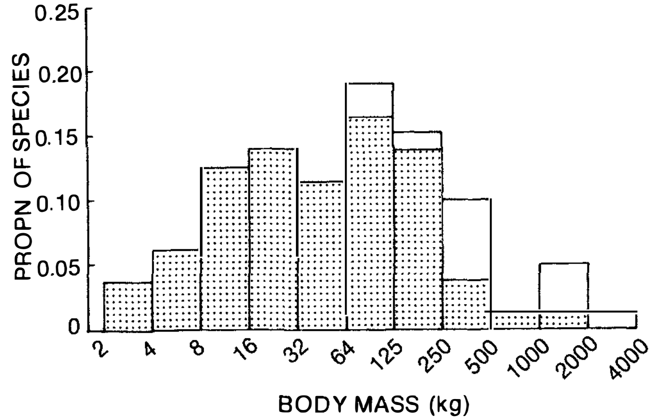

Fig. 17.1 Distribution of sub-Saharan African species of large herbivore among different body size ranges (N = 79 species). Shaded = ruminants, unshaded = non-ruminants. Taken from species listed in Macdonald (1984).

ruminants with individually specialized but complementary diets. The other adaptive peak is made up by a few megaherbivore species, exhibiting a fairly generalized tolerance for a wide range of vegetation components and habitat types.

These adaptive modes are based on alternative digestive strategies for utilizing the energy content of plant cell walls. The ruminant strategy achieves a high efficiency of microbial degradation of cell wall through compartmentalization of the foregut region, connecting orifices being designed to delay passage until a certain degree of breakdown of food residues has been achieved. Remastication of the ingested herbage is an important aid to this end. The megaherbivore strategy is to obtain a sufficiently long retention time for cell wall fermentation simply as a consequence of the allometry of large size, with relatively minor structural modifications of the gut. This route is especially readily followed by cecalids. In fact non-ruminants appear to fall within three quite distinct size ranges: (i) a size of about 100 kg, made up by largely omnivorous suids (plus, on other continents, tapirs and peccaries); (ii) a size range of 250–500 kg, within which zebras and other equids, having a fast passage rate of moderately well digested herbage, are concentrated; (iii) megaherbivores, which approach the digestive efficiency of ruminants. It is at a body mass of about 1000 kg that the mean retention time of the digesta in cecalids becomes similar to that achieved by many medium-sized ruminants.

Distinctions between grazers, subsisting mostly on grasses and similar fine-leaved, slowly fermenting plants, and browsers, eating the foliage and

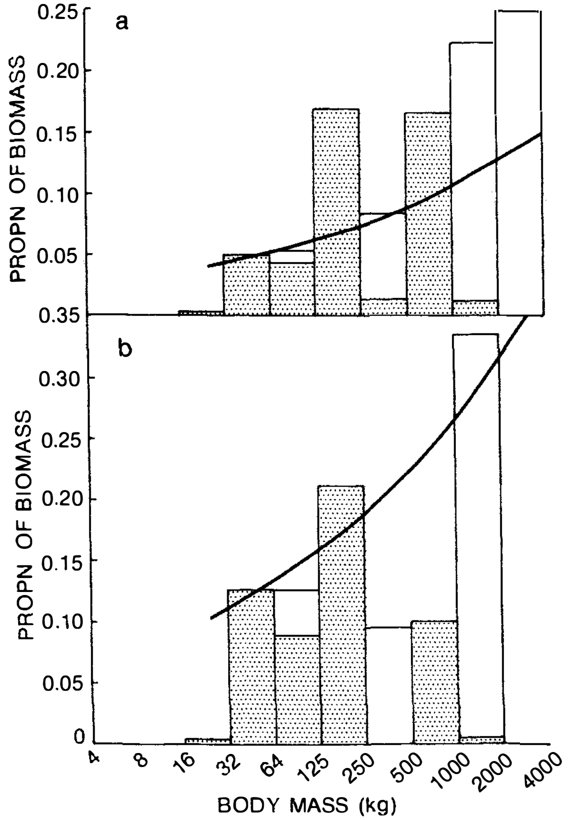

Fig. 17.2 Distribution of the combined population biomass of large herbivore species among different body size ranges. Curves indicate allometric trend in relation to $M^{0.25}$. (a) Amalgamated data from 18 conservation areas in African savanna regions (as listed in Fig. 14.3). (b) Local data for the Umfolozi–Hluhluwe Reserve in Natal, based on the helicopter census totals for 1970 corrected on the basis of intensive ground counts of sample areas for smaller species (see Table 12.1).

supporting stems of woody and herbaceous dicotyledons and non-graminaceous monocotyledons, exist among megaherbivores as they do among smaller ungulates. Despite including a high proportion of grass parts in their year-round diets, both surviving elephant species are basically browsers in their dietary adaptations. When feeding on grasses they select either young leaves or underground parts where soluble carbohydrates are stored, rather than leaves of all ages as grazers like white rhinos and hippos do. Among extinct megaherbivores there were likewise species adapted for either grass or woody browse diets. Specialist grazers were represented among most orders, including in particular mammoths among the elephants. Browsers were prevalent among rhinoceroses and ground sloths. Thus rumen microbial fermentation is not a necessary mechanism for detoxification of the secondary metabolites that are particularly a feature of dicotyledonous plants.

Large size confers other nutritional advantages. Because of the decrease in mass-specific metabolic rate as body size increases, very large animals can subsist on somewhat lower quality forage than smaller animals. As a result, a higher fraction of vegetation becomes nutritionally acceptable food, thereby expanding the food resource base. For the same reason, very large mammals can survive for somewhat longer on a starvation diet than could smaller animals. This provides a mechanism for bridging periods in the annual cycle when food availability is inadequate to meet maintenance requirements. Specific adaptations of food-gathering structures, such as wide mouths or nasal appendages in the form of trunks, may be necessary to enable very large animals to maintain an adequate rate of food intake where standing plant biomass is low. As an outcome of these adaptive features, the geographic ranges of many species of megaherbivore were exceptionally vast. Species such as the African elephant represent supreme examples of habitat generalists.

Lastly, very large size is advantageous for avoiding predation after maturity. Notably, female giraffe, which generally attain a body mass of about 800 kg, are susceptible to lion predation; while black rhinos, which generally weigh over 1000 kg, incur very little predation as adults.

All of these factors provide a suite of advantages to large body size, which come into operation above a body mass threshold of 1000 kg. This explains the trends towards attainment of such large size that are commonly evident among lineages of cecalid herbivores in the fossil record.

Social and life history patterns

With freedom from predation as adults, selective pressures towards group formation are reduced. Thus while medium-sized ungulates commonly form large herds, megaherbivores are typically solitary as adults, although temporary associations may be formed among immature animals. However, where species move over vast and changing home ranges, there are additional benefits for young animals in remaining associated with experienced matriarchs. This leads to the formation of persistent family units by modern elephants and perhaps also by the extinct mammoths.

Once body mass exceeds 1000 kg, gestation time generally exceeds one year. This feature, plus the fact that critical stages of offspring nutrition tend to be stretched through different times of the year, results in reproduction being largely decoupled from the seasonal cycle. Nevertheless, proximate effects of maternal nutrition on ovarian activity remain; in particular ovulation is suppressed during times when food intake is at submaintenance levels. Hence births may be concentrated in certain seasons of the year, but these seasons differ for different species of megaherbivore depending on gestation time. Birth intervals and time to sexual maturity extend over several years. Both maternal conceptions and growth of the young towards maturity may be deferred when conditions are unfavorable, leading to some plasticity in the timing of these critical life history features.

Because of the extended lifespan, males in particular may defer attainment of sexual maturity. Males furthermore exhibit various social strategies to decrease the incidence of damaging combats during adulthood, which may take the form of either spatial or temporal restrictions on dominance. A corrolary of large size is that fighting success becomes strongly dependent on power rather than on agility, promoting a marked size dimorphism between males and females in many species of megaherbivore. Females commonly exhibit behavioral patterns during courtship which allow them to exert some choice over mates, which may serve to eliminate male phenotypes that are not synchronously adapted to prevailing conditions.

If maternal investments in reproduction are related to resting metabolic rates, and allowance is made for neonatal survival, megaherbivores appear no more *K*-selected than other medium-sized ungulates in the tropics. Among megaherbivores, hippos appear relatively more *r*-selected for their size than either rhinoceroses or elephants, which may be a consequence of the restricted habitats that hippos are forced to occupy on account of their semi-aquatic habits. The overall time scaling of reproductive events appears related directly to potential lifespan, so that the maximum number of offspring that a female megaherbivore can produce is similar to the potential maximum for smaller ungulates giving birth to single young.

Demographic patterns

As a consequence of 2–4 year birth intervals, the maximum rates of growth in numbers of megaherbivore populations lie in the range 6–10% per annum. Hence populations may take a long time to recover from depression, in particular that caused by past human hunting. In effect the time scaling of population dynamics is shifted to a supra-annual scale. Even where reproduction is suppressed in one year, the effects only become apparent in reduced recruitment some years later. Thus populations exhibit considerable inertia in responding to events occurring on a one or two year time scale, although they may respond to longer term cycles in climate or habitat conditions.

While predation may commonly depress populations of medium-sized herbivores somewhat below the ultimate limits set by environmental resources, megaherbivore populations tend towards saturation densities at which further increase becomes restricted directly by nutritional limitations. These nutritional restrictions manifest themselves in terms of greatly extended birth intervals and deferred attainment of maturity. Population stasis may thus be achieved with relatively minor increases in mortality rates, at least among adults.

Dispersal movements by medium-sized ungulates are largely sex-specific and thus related to inbreeding avoidance. However, among megaherbivores dispersal is important as a fast-acting response to redistribute populations in relation to changing resource distributions, and is thus commonly shown by both sexes. In particular, dispersal movements enable animals to avoid situations where local resource depression may become severe enough to precipitate starvation mortality during short term droughts. However, if such movements are prevented by fences or human disturbance, population crashes can result, although such episodes would have been much less frequent for megaherbivores than they are for smaller species in the absence of such spatial restrictions.

Having evolved in the absence of significant predation on adults, megaherbivore populations do not have the capability to sustain the levels of harvest that can potentially be inflicted by organized bands of skilled human hunters. Thus a wave of extinctions of megaherbivores spread through Eurasia as humans expanded their range northwards during the course of the late Pleistocene, and then lept southwards through the Americas in a brief blitz following the entry of these skilled hunters. Megaherbivores survived only in Africa and in tropical Asia, where they were not hunted to any significant extent during the Pleistocene, perhaps because species had coevolved as human hunters gradually increased their competency as predators on large mammals. This situation has now changed as humans with modern weapons exploit remaining elephant and rhino populations for their ivory and horns.

Community and ecosystem patterns

Megaherbivores typically form at least half of the total biomass of large herbivores, and account for about half of the energy metabolized through the large herbivore community. Their impact on vegetation structure and composition can far outweigh that of smaller herbivores.

In the absence of predation, sustained grazing pressure by medium-sized grazers or browsers may depress plant populations, in particular by suppressing reproduction, either in terms of seed production or seedling survival. Concentrated trampling may amplify such effects, in particular around water points or other localities where animals concentrate. Because of their dietary fiber tolerance, megaherbivores can exert a somewhat greater impact on mature plants, and besides feeding they cause additional breakage to such trees or grasses. Thereby they can induce major transformations of vegetation structure. Savanna woodlands may be transformed into coppice regrowth, while medium-height savanna grasslands are converted into a mosaic of short grass areas. Through such effects megaherbivores can accelerate the recycling of the nutrients locked up in plant structural tissues. The result may be the transformation of high biomass, low productivity and low nutrient content vegetation communities into regenerating communities with a much greater production of better quality plant types and tissues. A mosaic interspersion of habitats at different stages of regeneration may be created.

While such structural changes are largely beneficial to the feeding of megaherbivores, other effects may be detrimental. Reserve food sources used during droughts may be severely damaged or eliminated, making them unavailable for such emergencies in the future. Fire may interact with elephant damage to eliminate woody plant regeneration, particularly on clayey soil substrates. However, in the past when the impacts of both browsing and grazing megaherbivores were coupled in the same areas, fire could have played a much reduced role than it does now, although there would always have been regions far from water where fire would have been the main consumer of accumulated plant biomass.

By promoting lowered and more nutrient-rich vegetation, and a higher mosaic diversity of habitats, the impacts of megaherbivores on vegetation are by and large favorable for smaller species of herbivore. Nevertheless, some species may be affected adversely by structural changes in vegetation cover induced by megaherbivores. Elimination of megaherbivore impact on vegetation was probably an important precipitating factor in the late Pleistocene extinctions of large mammalian species in the Americas and northern Eurasia. The kinds of forest and grassland formations that occur in North and South America today are probably very different from those that prevailed during the Pleistocene and earlier times in the presence of abundant megaherbivores, including both grazers and browsers.

Conservation

At the time of writing those megaherbivore species that survived the late Pleistocene extinctions in Africa and tropical Asia are declining rapidly due to resurging exploitation, as well as human competition for space. Within conservation areas where dispersal is inhibited by fencing or surrounding human activities, megaherbivores could induce progressive habitat changes that would eventually become inimical to the persistence of other animal and plant species. The pre-emptive culling programs carried out by some conservation authorities generate much anxious debate among the public from both ecological and animal welfare considerations. At the same time, many pragmatic conservationists contend that the only workable basis for conserving such large and destructive animals in Third World countries is through economic exploitation for products such as ivory.

The message from this book is that such economic exploitation can be sustained only if it is exceptionally tightly controlled, because of the low rates of harvest that megaherbivore populations can support. Over much of the Africa of today the prospects for achieving such control are somewhat dismal, given the conditions of rural impoverishment and political instability that are widely prevalent. The situation in tropical Asian countries is not that much better. Populations of rhinoceroses in particular are plumetting rapidly to levels where genetic inbreeding becomes a major threat to the long term viability of the remaining remnants. Elephant numbers are undergoing progressive attrition. Only hippos and giraffes are not currently a source of concern: hippos because of their aquatic daytime refuges, from which they are difficult to harvest; and giraffe – which fall questionably into the megaherbivore category – because they currently offer no valuable products.

I hope that this book arouses a full appreciation of the rich biology of these giants among our fellow inhabitants of this planet, and of the important messages for us from their biology. For today *Homo sapiens* has usurped the megaherbivore role over most of the planet. While much of the habitat transformation induced by human activities has been beneficial to our food resource base, opportunities for dispersal across oceans have been instrumental in alleviating short term situations of resource depletion. The stage is now being reached where all productive habitats are becoming saturated; and under such conditions the resource reserves that might be needed for future crises are being rapidly eliminated. Unless we learn from the messages of the past, our future viability as a species might be no more hopeful in the long term than it is for elephants and rhinos.

Appendix I

Scientific names, abbreviations and body mass data for mammal species referred to in the text, tables and figures

Mean and maximum live mass reported for sexually mature animals of each sex are given (where sufficient data are available). A range of values is indicated where body mass varies significantly between different populations of the species. Figures in brackets represent guestimates. The asymptotic body mass for each sex is taken to be the average of the mean and maximum masses. The population mean mass per individual for all age classes is taken to be three-quarters of the mean adult female mass.

Table I.1

Species	Abbreviation	Body mass (kg) Ad♀ mean/max	Body mass (kg) Ad♂ mean/max	Source
Ass, African wild *Equus asinus*	WA	(200)	(200)	—
Ass, Asian wild *Equus hemionus*	AA	(145)	(145)	8
Barasingha *Cervus duvauceli*	Bar/Ba	145	212/260	36
Bison, American *Bison bison*	Bi	495	808/907	26
Blackbuck *Antilope cervicapra*	Bla	35/39	38/43	36
Blesbok *Damaliscus dorcas phillipsi*	Bl	60/86	70/100	7,28,40
Bontebok *Damaliscus d. dorcas*	Bo	55	61/64	40
Buffalo, African *Syncerus caffer*	AB	520/636	650/860	13,33,35,38,43
Buffalo, water *Bubalus bubalis*	WB	—	(450)	—
Bushbuck *Tragelaphus scriptus*	Bb	30–44/34–45	45–55/54–59	15,30,40
Bushpig *Potamochoerus porcus*				
Camel, Bactrian *Camelus bactrianus*	Ca	545	—	8
Camel, dromedary *Camelus dromadarius*	Ca	545	545	8

Caribou *Rangifer tarandus groenlandicus*	Cu	90	180	46
Cattle *Bos taurus/indicus*	C	(450)	(450)	—
Cheetah *Acinonyx jubatus*				
Deer, mule *Odocoileus hemionus*	MD	55	84/120	45,46
Deer, red *Cervus elaphus*	ReD/Red	90	120–160/299	29,46
Deer, roe *Capreolus capreolus*		22	23	46
Deer, spotted *Axis axis*	SD/SpD	50	86	36,46
Deer, white-tailed *Odocoileus virginianus*	WD	52	86/136	45,46
Dikdik *Madoqua kirkii*	Di	4.0–5.3/6.5	4.0–5.1/6.0	15,35,40
Dog, African hunting *Lycaon pictus*				
Duiker, blue *Cephalophus monticola*	BD	4.7	4.2	40
Duiker, grey *Sylvicapra grimmii*	GD	12–21/17–25	12–19/17–21	15,40,43
Duiker, red *Cephalophus natalensis*	RD	14/18	14/17	17,40
Eland *Taurotragus oryx*	El	320–445/370–470	500–605/570–945	12,28,40,44
Elephant, African *Loxodonta africana*	AE	2800/4000	5000/8000	11,21,22,40,43
Elephant, Asian *Elephas maximus*	IE	2500/4160	4000/5400	37

Table I.1 (*cont.*)

Species	Abbreviation	Body mass (kg) Ad♀ mean/max	Body mass (kg) Ad♂ mean/max	Source
Elk, American *Cervus canadensis*	Ek	250	290–350	9,46
Gaur *Bos gaurus*	Gau	590/700	880/940	36
Gazelle, Grant's *Gazella granti*	GG	45/67	65/81	19,35
Gazelle, Thomson's *Gazella thomsoni*	TG	17–20/23	21–23/29	19,23,35
Gerenuk *Litocranius walleri*	Ge	30/45	40/52	15,19,24
Giraffe *Giraffa camelopardalis*	Gi	825/1125	1200/1400	40,43
Goat *Capra hircus* domesticated	G	(40)	—	—
Goat, Rocky mountain *Oreamnos americanus*				
Guanaco *Lama guanicoe*	Gu	90	90	8
Hartebeest, Coke's *Alcelaphus buselaphus cokei*	CH/Ha	125/135	140/196	15,35,42
Hartebeest, Lichtenstein's *Alcelaphus lichtensteini*	LH	166/181	177/204	40
Hartebeest, red *Alcelaphus buselaphus caama*	RH/Ha	120/136	152/156	40

Hippopotamus *Hippopotamus amphibius*	Hi	1350/2311–2352	1500/2143–2669	3,27,28,40,43
Hippopotamus, pigmy *Choeropsis liberiensis*	PH	(160)	(200)	8
Horse, domestic *Equus caballus*	H	320	350	—
Hyena, (spotted) *Crocuta crocuta*				
Impala *Aepyceros melampus*	Im	40–48/54	55–63/76	13,15,35,40
Klipspringer *Oreotragus oreotragus*	Kl/Ks	13/17	11/17	28,40,43
Kob *Kobus kob*	Ko	63/77	94/121	15,23
Kudu, lesser *Tragelaphus imberbis*	LK/Lk	56/83	92/108	15,24,25
Kudu, (greater) *Tragelaphus strepsiceros*	GK	170/204	257/286	18,43
Lechwe *Kobus leche*	Le	80/97	105/129	40
Moose *Alces alces*	Mo	343–448	430–550	2,46
Muskox *Ovibos moschatus*				
Nilgai *Boselaphus tragocamelus*	Ni	120	240	45
Nyala *Tragelaphus angasi*	Ny	63/80	107/143	13,40
Oribi *Ourebia ourebi*	Or/Oi	10–16/17–20	10–16/17–21	15,28,31,40

Table I.1 (*cont.*)

Species	Abbreviation	Body mass (kg) Ad♀ mean/max	 Ad♂ mean/max	Source
Oryx *Oryx gazella*	Oy	162–210/188–227	176–235/209–240	24,39,40
Peccary, collared *Dicotyles tajacu*				
Pronghorn *Antilocapra americana*				
Puku *Kobus vardoni*	Pu	65/78	75/84	40,43
Reedbuck, Bohor *Redunca redunca*	BRb	40/55	49/65	15,19
Reedbuck, (southern) *Redunca arundinum*	Rb	38–54/51–64	52–80/68–104	19,39,40,43
Reedbuck, mountain *Redunca fulvorufula*	MR	22–29/35	25–30/38	15,19,40
Reindeer *Rangifer tarandus*	Rd	100	—	45
Rhebuck, grey *Pelea capreolus*	GR	25	25	31
Rhinoceros, black *Diceros bicornis*	BR	932–1080/1134–1316	931–1124/1022–1316	14,28
Rhinoceros, Indian *Rhinoceros unicornis*	IR	1600	2100	20
Rhinoceros, Javan *Rhinoceros sondaicus*	JR	(1300)	(1300)	—
Rhinoceros, Sumatran *Dicerorhinus sumatrensis*	SR	(800)	(800)	10

Rhinoceros, white *Ceratotherium simum*	WR	1600/1800	2200/2400	this book
Roan, antelope *Hippotragus equinus*	RA	260/280	280/300	43
Sable, antelope *Hippotragus niger*	SA	220/232	235/263	43
Sambar *Cervus unicolor*	Sam	165	285/350	36
Sheep, Dall *Ovis canadensis dalli*	DS	—	100	8
Sheep, domestic *Ovis aries*	S	45	—	—
Sheep, Soay *Ovis aries* feral	SS	25	35	5
Springbok *Antidorcas marsupialis*	Sp/Sb	28–35/32–43	32–42/35–48	32,34,40
Steenbok *Raphicerus campestris*	St	11/14	11/15	15,28,40
Suni *Nesotragus moschatus*	Su	5.4/8.2	5.0	16,40
Tapir, American *Tapirus terrestris*	AT	135	160	8
Tapir, Asian *Tapir indicus*	IT	(160)	275	8
Thar, Himalayan *Hemitagus jemlahicus*				
Topi *Damaliscus lunatus korrigum*	To	100/131	120/152	6,28,35
Tsessebe *Damaliscus l. lunatus*	Ts	127/144	140/155	40

	Body mass (kg)		
Abbreviation	Ad♀ mean/max	Ad♂ mean/max	Source
Wh	58/76	80/107	13,24,35,40,43
Wb/Wa	180/214	240/287	13,24,35,41,43
Wi	163–223/209–253	210–252/271–295	1,4,13,24,35
BW	140	180	40
GZ	380/450	400/450	19,23
MZ	235–276/257–300	300/350	40
BZ	220–310/242–330	250–320/284–340	35,40,43

ttwell 1982; 2 – Belovsky & Jordan 1978; 3 – Bere 1959; 4 – Berry, 1980; 5 – Doney *et al.* 1974;
Plessis 1972; 8 – Foose 1982; 9 – Greer & Howe 1964; 10 – Groves & Kurt 1972; 11 – Hanks 1972b;
Hitchins 1968; 14 – P. M. Hitchins personal communication 1983; 15 – Hofman 1973; 16 – Hoppe 1977b;
18 – Huntley 1971; 19 – Kingdon 1982; 20 – Laurie 1982; 21 – Laws 1966; 22 – Laws *et al.* 1975;
edger 1964; 25 – Leuthold 1979; 26 – Lott 1979; 27 – Mackie 1973; 28 – Meinertzhagen 1938;
30 – Morris & Hanks 1974; 31 – Oliver *et al.* 1978; 32 – Penzhorn 1974; 33 – Pienaar 1969; 34 – Robinson
6 – Schaller 1967; 37 – Shoshani & Eisenberg 1982; 38 – Sinclair 1977; 39 – Smithers 1971; 40 – Smithers
42 – Stanley-Price 1974; 43 – Wilson 1968; 44 – Wilson 1969a; 45 – Macdonald 1984; 46 – Geist & Bayer 1988.

Appendix II

Simulation model of the white rhino population

The model was formulated in PASCAL for implementation on an Apple II microcomputer. The basis of the model is a population made up of 46 year groups, which were grouped into functional age classes differing in their mortality, natality and dispersal rates. The age classes were as follows: old – 36–45 y; adult – 11–35 y; subadult – 6–10 y; immature – 3–5 y; juvenile – 1–2 y; infant – 0 y.

The sex ratio was considered to be 50:50 throughout all age classes. Demographic parameters operated on the year groups in the following order: first emigration, then mortality, then natality. Thus the number of animals entering age group 0 was calculated by multiplying the number of females surviving within the age classes, OLD, ADULT and SUBADULT by the age-class specific natality rates, by a factor of 0.5 to adjust for the sex ratio, and finally by the infant survival rate.

(a) Simple model of expanding and stable populations

In the initial use of the model in Chapters 11 and 13, fixed values were assigned to demographic parameters as in Table II.1 (all rates expressed per annum):

Table II.1

Variable	Expanding population	Stable population
EMIGRATION	0	0
OLDMORT	0.05	0.08
ADMORT	0.015	0.03
SAMORT	$0.5 \times (0.015 + 0.03)$	$0.5 \times (0.03 + 0.06)$
IMMORT	0.03	0.06
JUVMORT	0.035	0.08
INFMORT	0.08	0.24
OLDNATAL	0.30	0.15
ADNATAL	0.40	0.25
SANATAL	0.45	0.07

The class of subadults is assumed to operate as a mix of males, still exhibiting immature mortality rates, and females exhibiting adult mortality rates. Subadult females have a varying natality rate depending on the age at first parturition; a natality of 0.07 means that females first give birth in year class 10.

Arbitrary starting numbers were chosen for each year group, and iteration was carried out over a 100 year period to allow the age structure to stabilize.

(b) Density dependent demographic variables

In the logistic formulation the rate of population increase is a function of the factor $(1 - N/K)$, where K is a constant representing the asymptotic density of the population, and N is a variable representing the population density. Caughley (1976c) suggests that, for plant–herbivore systems, K reflects the amount of edible and accessible food available, and N reflects the rate at which it is used up by the population. Hence the ratio K/N represents the amount of food available per unit of herbivores. At the asymptotic density, the rate of food gained by the herbivore population is just adequate for rates of recruitment to balance rates of loss.

In the absence of dispersal the net rate of population increase is simply the difference between the overall birth rate (B) and death rate (D). In the logistic formulation these component rates are linearly related to N, i.e. $B = B_{\max} - aN$ and $D = D_{\min} + cN + P$, where a and c are constants, and P represents the density-independent component of mortality. The density K is the point where these lines intersect, i.e. $B = D$. When N is zero, $B = B_{\max}$ and $D = D_{\min}$, and the maximum or intrinsic rate of population increase, $R_{\max}$, is given by the difference $B_{\max} - D_{\min}$ (see Pianka 1974, p. 86).

However, for a realistic population model the simple linear dependence of mortality and natality rates on population density needs to be modified. Firstly, following Caughley's interpretation, mortality and natality rates will be related to the ratio K/N rather than to N. Secondly, because of the wide difference in individual weights, K and N will be expressed in terms of biomass rather than density. Thirdly, lower and upper bounds for mortality and natality respectively, reached at some biomass below K, will be introduced. Fourthly, where mortality rates are as low as they are in white rhinos their values increase too slowly, over the range of densities in excess of K, with a linear formulation, to generate the starvation induced mortality which must eventually set in at high biomass levels. Potential alternative formulations include (i) a breakpoint, with a steeper rate of increase in mortality once populations exceed this threshold density; (ii) a power function relating mortality to biomass. In the white rhino model the latter function will be assumed.

In order to formulate specific functions for demographic variables, values for at least two points are needed. Mortality and natality rates were known for the real white rhino population in 1970, when it was increasing at near its maximal rate. A realistic combination of changed values which would achieve population stasis was found by trial and error. However, the biomass level at which the latter values would prevail was unknown. Arbitrarily it will be assumed that, with no depression of grass production and with no emigration, the white rhino population would tend to stabilize at a biomass about 50% higher than that prevailing in 1970; i.e. a mean biomass (M) of 6500 kg km^{-2} over the 450 km^2 area of UGR. Thus at $M = 0.67\ K$, the 1970 values for mortality and natality rates prevail. At $M = K$, the values producing population stasis prevail, where $K = 6500$ kg km^{-2}. Based on these two points, functions relating demographic variables to the ratio K/M were derived, where M represents the prevailing population biomass. Because of physiological lags due to accumulated body reserves, the demographic responses of adults were taken to be functions of biomass levels over the preceding three year period, those of juveniles to depend on biomass levels over the preceding two years, while infant mortality responds directly to the currently prevailing conditions. Because of its dependence on growth rates, subadult natality will be related to mean biomass over a five year period.

Emigration rates are difficult to estimate. During the phase of white rhino population increase, emigration rates of 3% per annum for adult males and 7.5% per annum for subadults were indicated (Chapter 11). It will be assumed that these represent individuals dispersing out of saturated zones, and that 75% of the population occurred in such high density zones. Thus at saturation densities dispersal rates are estimated to be 5% per adult male per year, or 2.5% per adult per year (assuming a 50:50 sex ratio), and 10% per subadult or immature per year. At two-thirds of the saturation biomass, dispersal rates are assumed to be about half of the above values. At biomasses in excess of the saturation biomass, some adult females with calves start dispersing. Emigration rates will be assumed to depend on currently prevailing conditions with no lag effects. In the model, emigration may be either allowed or prevented as an option at the beginning of the run. The functions used for demographic variables in the white rhino model are given in Table II.2, where M represents the prevailing population biomass the preceding year, $M2$ represents the mean population biomass over the preceding two years, $M3$ represents the mean population biomass over the preceding three years, and $M5$ represents the mean population biomass over the preceding five years:

Table II.2

Variable	Function	Upper or lower bound
OLDMORT	$\exp(-2.526-1.159\times\ln(K/M3))$	0.05
ADMORT	$\exp(-3.507-1.709\times\ln(K/M3))$	0.01
IMMORT	$\exp(-2.813-1.709\times\ln(K/M3))$	0.02
SAMORT	$(0.5\times\mathrm{ADMORT}+\mathrm{IMMORT})$	
JUVMORT	$\exp(-2.526-2.039\times\ln(K/M2))$	0.02
INFMORT	$\exp(-1.427-2.709\times\ln(K/M))$	0.05
OLDNATAL	$-0.15+0.30\times(K/M3)$	0.35
ADNATAL	$-0.05+0.30\times(K/M3)$	0.45
SANATAL	$-0.75+0.80\times(K/M5)$	0.50
ADEMIGR	$-0.01+0.03/(K/M)$	0
IMEMIGR	$-0.05+0.15/(K/M)$	0
SAEMIGR	$-0.05+0.15/(K/M)$	0
JUVEMIGR	$-0.02+0.02/(K/M)$	0

The bounds for mortality and natality rates have been set slightly lower and higher respectively than the rates prevailing in the 1970 population. Thus the model population has an intrinsic rate of increase of 10.5% per annum.

(c) Vegetation interaction

Caughley (1982) showed that a many-plant system could be modelled as if it consisted of a single plant species whose rate of increase was the harmonic mean of the specific rates of increase of each component species. Hence a simple logistic equation will be used to represent all grasses.

No grass production measurements are available for Umfolozi. Based on measurements carried out at the Matopos research station in Zimbabwe (Dye 1983), and at Nylsvley in the northern Transvaal (Grunow *et al.* 1980), the saturation biomass of grass was taken to be 200 g m^{-2}. Not all of this would be available for consumption by white rhinos. The consumptive demands of other grazing ungulates combined are about equal to those of white rhinos, and to this has to be added the grass removed by insects such as grasshoppers and harvester termites. On a regional basis some grassland areas are relatively inaccessible to white rhinos, for example on steep hillsides or in thickets. It will be assumed that, of the total grass production, 65% is consumed by other herbivores, while 30% of the remainder is inaccessible to white rhinos, so that the amount available for white rhino consumption is 50 g m^{-2}.

The food demands of white rhinos amount to 1.5% of body mass (drymass/livemass) per day, or five times the standing biomass of white rhinos over the course of a year. Some reduction in eating rates at low grass biomass will be allowed according to a type 2 curve of Holling (1965). Thus

EATRATE: = 5 × (2 × VHFACTOR/1 + VHFACTOR)
if VHFACTOR < 1

where VHFACTOR represents the quantity of grass available per white rhino, as determined by the factor (grass biomass)/(white rhino biomass), normalized to vary between 1 and 0.

Based on standard agricultural recommendations, the threshold for overutilization of grass will be taken as 50% of available grass production. If the white rhino population consumes less than this proportion, they have no influence on future grass production (i.e. they simply remove part of the annual growth, which is replaced completely the next season). If the consumptive demands of the white rhino population exceed this threshold utilization, the grass population is depressed to the extent that consumption exceeds this threshold; thus

GRASS: = GRASS × (1–XSUTIL)

where GRASS represents the grass population, and XSUTIL the fraction by which consumption exceeded the 50% threshold. However, the depressed grass population then grows back at the rate given by the logistic equation. To prevent the grass population going to extinction, an ungrazable reserve amounting to 20% of the saturation biomass of grass is incorporated.

(d) Variable rainfall regime

In the preceding formulation the annual grass biomass was assumed to be constant, apart from the influence of white rhino consumption. However, grass production is influenced by rainfall, and for rainfall regimes below 700 mm per year annual grass production is almost linearly related to the current season's rainfall (Dye 1983). Thus to obtain the amount of grass produced in a particular year, the potential saturation biomass of grass is multiplied by the ratio (annual rainfall/mean rainfall).

(e) Medium-sized ungulate

To simulate a population of medium-sized ungulates, for example wildebeest, the main changes made to the model were as follows: (i) the number of year groups was reduced; (ii) different upper or lower bounds were chosen for demographic variables; (iii) new values of demographic variables that would yield a static population in the absence of dispersal were found; (iv) the period over which biomass was averaged in the functions for demographic variables was reduced. The differences in parameter values between the two versions of the model are listed in Table II.3. For demographic variables the value for a static population is given first, followed by the upper or lower bound in brackets, expressed per annum:

Table II.3

Parameter or variable	White rhino	Wildebeest
Unit adult body mass (kg)	1600	180
Saturation biomass	6500	4643
Eating rate (% per day)	1.5	2.0
Age ranges (y):		
Old	36–45	11–15
Adult	11–35	3–10
Subadult	6–10	2
Immature	3–5	1
Juvenile	0–2	0
OLDMORT	0.08 (0.05)	0.20 (0.05)
ADMORT	0.03 (0.01)	0.08 (0.03)
IMMORT	0.06 (0.02)	0.16 (0.04)
JUVMORT	0.08 (0.02)	0.50 (0.06)
INFMORT	0.24 (0.05)	
OLDNATAL	0.15 (0.30)	1.00 (1.00)
ADNATAL	0.25 (0.45)	1.00 (1.00)
SANATAL	0.05 (0.50)	0 (1.00)
ADEMIGR	0.02 (0.05)	0.02 (0.04)
IMEMIGR	0.10 (0.25)	0.10 (0.20)
JUVEMIGR	0 (0.02)	0.01 (0.02)
Biomass averaging period (y):		
Adults	3	2
Immatures	2	1
Juveniles	1	1
Subadult natality	5	3
R_{max} (% per year)	10.5	30.0

References

Agenbroad, L. D. (1984). Hot Springs, South Dakota: entrapment and taphonomy of Columbian mammoth. In *Quaternary Extinctions*, ed. P. S. Martin & R. G. Klein, pp. 113–27. Tucson, Arizona: University of Arizona Press.

Alexandre, D.-Y. (1978). Le role disseminateur des elephants en foret de Tai, Cote D'Ivoire. *La Terre et la Vie*, **32**, 47–72.

Allen-Rowlandson, T. S. (1980). The social and spatial organisation of the greater kudu in the Andries Vosloo Game Reserve, Eastern Cape, M.Sc. thesis, Rhodes University, Grahamstown.

Anderson, A. (1984). The extinction of moa in southern New Zealand. In *Quaternary Extinctions*, ed. P. S. Martin & R. G. Klein, pp. 691–707. Tucson, Arizona: University of Arizona Press.

Anderson, E. (1984). Who's who in the Pleistocene: a mammalian bestiary. In *Quaternary Extinctions*, ed. P. S. Martin & R. G. Klein, pp. 40–89. Tucson, Arizona: University of Arizona Press.

Anderson, G. D. & Walker, B. H. (1974). Vegetation composition and elephant damage in the Sengwa Research Area, Rhodesia. *J. Sth. Afr. Wildl. Mgmt. Ass.*, **4**, 1–14.

Anderson, J. L. (1978). Aspects of the ecology of nyala in Zululand. D. Phil. thesis, London University, London.

Anderson, J. L. (1980). The social organization and aspects of behaviour of the nyala. *Z. Saugetierk*, **45**, 90–123.

Anderson, J. L. (1983). Sport hunting in national parks: sacrilege or salvation? In *Management of Large Mammals in African Conservation Areas*, ed. R. N. Owen-Smith, pp. 271–280. Pretoria: Haum.

Ansell, W. F. H. (1963). Additional breeding data on Northern Rhodesian mammals. *Puku*, **1**, 9–28.

Arman, P. & Field, C. R. (1973). Digestion in the hippopotamus. *E. Afr. Wildl. J.*, **11**, 9–18.

Arman, P. & Hopcraft, D. (1975). Nutritional studies in East African herbivores. Digestibilities of dry matter, crude fibre and crude protein in antelope, cattle and sheep. *Brit. J. Nutr.*, **33**, 255–64.

Attwell, C. A. M. (1977). Reproduction and population ecology of the blue wildebeest in Zululand. Ph.D. thesis, University of Natal, Pietermaritzburg.

Attwell, C. A. M. (1982). Growth and condition of blue wildebeest in Zululand. *S. Afr. J. Wildl. Res.*, **12**, 63–70.

Attwell, C. A. M. & Hanks, J. (1980). Reproduction of the blue wildebeest in Zululand, South Africa. *Saugetierk. Mitt.*, **28**, 264–81.

Backhaus, D. (1959). Beobachtungen uber das Freileben von Lelwel-Kuhantelopen und Gelegenheit-Beobachtungen an Sennar-Pferdeantilopen. *Z. Saugetierk.*, **24**, 1–34.

Bainbridge, W. R. (1965). Distribution of seed in elephant dung. *Puku*, **3**, 173–5.

Barnes, R. F. W. (1979). Elephant ecology in Ruaha National Park, Tanzania. Ph.D. thesis, Cambridge University.

Barnes, R. F. W. (1980). The decline of the baobab tree in Ruaha National Park, Tanzania. *Afr. J. Ecol.*, **18**, 243–52.

Barnes, R. F. W. (1982a). Elephant feeding behaviour in Ruaha National Park, Tanzania. *Afr. J. Ecol.*, **20**, 123–36.

Barnes, R. F. W. (1982b). Mate-searching behaviour of elephant bulls in a semi-arid environment. *Anim. Behav.*, **30**, 1217–23.

Barnes, R. F. W. (1982c). A note on elephant mortality in Ruaha National Park, Tanzania. *Afr. J. Ecol.*, **20**, 137–41.

Barnes, R. F. W. (1983a). The elephant problem in Ruaha National Park, Tanzania. *Biol. Cons.*, **26**, 127–48.

Barnes, R. F. W. (1983b). Effects of elephant browsing on woodlands in a Tanzanian national park: measurements, models and management. *J. Appl. Ecol.*, **20**, 521–40.

Barnes, R. F. W. (1985). Woodland changes in Ruaha National Park (Tanzania) between 1976 and 1982. *Afr. J. Ecol.*, **23**, 215–22.

Barnes, R. F. W. & Douglas-Hamilton, I. (1982). The numbers and distribution patterns of large mammals in the Ruaha-Rungwa area of southern Tanzania. *J. Appl. Ecol.*, **19**, 411–25.

Barrow, J. (1801). *An account of travels in the interior of Southern Africa, in the years 1797 and 1798.* London.

Bell, R. H. V. (1969). The use of herbaceous layer by grazing ungulates in the Serengeti National Park, Tanzania. Ph.D. thesis, University of Manchester.

Bell, R. H. V. (1970). The use of the herb layer by grazing ungulates in the Serengeti. In *Animal Populations in Relation to their Food Resources.* ed. A. Watson, Symp. Brit. Ecol. Soc., pp. 111–24. Oxford: Blackwell.

Bell. R. H. V. (1971). A grazing ecosystem in the Serengeti. *Sci. Amer.*, **225**, 86–93.

Bell, R. H. V. (1981a). An outline of a management plan for Kasungu National Park, Malawi. In *Problems in Management of Locally Abundant Wild Mammals*, ed. P. A. Jewell, S. Holt & D. Hart, pp. 69–89. New York: Academic Press.

Bell, R. H. V. (1981b). An estimate of nyala numbers in Lengwe National Park by estimating the drinking rates of recognisable animals. *Mimeogr. Rep.*, Dept. of National Parks & Wildlife, Malawi.

Bell, R. H. V. (1982). The effect of soil nutrient availability on community structure in African ecosystems. In *The Ecology of Tropical Savannas*, ed. B. J. Huntley & B. H. Walker, pp. 193–216. Berlin: Springer-Verlag.

Bell, R. H. V. (1984). Notes of elephant-woodland interactions. In *The Status and Conservation of Africa's Elephants and Rhinos*, ed. D. H. M. Cumming & P. Jackson, pp. 98–103. Gland, Switzerland: IUCN.

Belovsky, G. E. & Jordan, P. A., (1978). The time-energy budget of a moose. *Theor. Pop. Biol.*, **14**, 76–104.

Benedict, F. G. (1936). *Physiology of the elephant.* Carnegie Institute, Washington D.C., Publ. No. 474, 302 pp.

Bere, R. M. (1959). Queen Elizabeth National Park, Uganda. The hippopotamus problem and experiment. *Oryx*, **5**, 116–24.

Berger, J. (1981). The role of risks in animal combat: zebra and onager fights. *Z. Tierpsychol.*, **56**, 297–304.

Berry, H. H. (1980). Behavioural and eco-physiological studies on blue wildebeest at the Etosha National Park. Ph.D. thesis, University of Cape Town.

Berry, H. H., Siegfried, W. R. & Crowe, T. M. (1982). Activity patterns in a population of free-ranging wildebeest at Etosha National Park. *Z. Tierpsychol.*, **59**, 229–46.

Berry, P. S. M. (1978). Range movements of giraffe in the Luangwa Valley, Zambia. *E. Afr. Wildl. J.*, **16**, 77–84.

Bigalke, R. C. (1970). Observations on springbok populations. *Zoologica Africana*, **5**, 59–70.

Bigalke, R. C. (1972). Observations on the behaviour and feeding habits of the springbok. *Zoologica Africana*, **7**, 333–59.

Blankenship, L. H. & Qvortrup, S. A. (1974). Resource management on a Kenya ranch. *J. Sth. Afr. Wildl. Mgmt. Ass.*, **4**, 185–90.

Blueweiss, L., Fox, H,. Kudzama, V., Nakashima, D., Peters, R. & Sams, S. (1978). Relationships between body size and some life history parameters. *Oecologia*, **37**, 257–72.

Borner, M. (1979). A field study of the Sumatran rhinoceros. Ph.D. thesis, University of Basel.

Bosman, P. & Hall-Martin, A. (1986). *Elephants of Africa*. Cape Town: Struik.

Botkin, D. B., Mellilo, J. M. & Wu, L. S.-Y. (1981). How ecosystem processes are linked to large mammal population dynamics. In *Dynamics of Large Mammal Populations*, ed. C. W. Fowler & T. D. Smith, pp.373–88. New York: John Wiley.

Bourliere, F. (1961). Le sex-ratio de la Giraffe. *Mammalia*, **25**, 467–71.

Bourliere, F. (1965). Densities and biomasses of some ungulate populations in Eastern Congo and Ruanda, with notes on population structure and lion/ungulate ratios. *Zoologica Africana*, **1**, 199–207.

Bourliere, F. & Verschuren, J. (1960). *Introduction a l'ecologie des Ongules du Parc National Albert*. Brussels.

Boyce, M. S. (1979). Seasonality and patterns of natural selection for life histories. *Am. Nat.*, **114**, 569–83.

Bradbury, J. W. & Vehrencamp, S. L. (1977). Social organization and foraging in emballonurid bats. III Mating systems. *Behav. Ecol. Sociobiol.*, **2**, 1–17.

Brain, C. K. (1985). Temperature induced environmental changes in Africa as evolutionary stimuli. In *Species and Speciation*, ed. E. S. Vrba, pp. 45–52. Transvaal Museum Monograph No. 4, Pretoria: Transvaal Museum.

Brooks, P. M. (1974). The effect of extensive removals on the population composition of the square-lipped rhinoceros in the H.G.R.–Corridor–U.G.R. Complex in Zululand, and recommendations on the age and sex ratios of future removals. Unpublished report, Natal Parks Board.

Brooks, P. M. & Macdonald, I. A. W. (1983). An ecological case history of the Hluhluwe–Corridor–Umfolozi Game Reserve Complex, Natal, South Africa. In *Management of Large Mammals in African Conservation Areas*, ed. R. N. Owen-Smith, pp. 51–78. Pretoria: Haum.

Brown, J. H., Davidson, D. W., Munger, J. C. & Inouye, R. S. (1986). Experimental community ecology: the desert granivore system. In *Community Ecology*, ed. J. Diamond & T. J. Case, pp.41–62. New York: Harper & Row.

Brown, J. H. & Maurer, B. A. (1986). Body size, ecological dominance and Cope's rule. *Nature*, **324**, 248–50.

Brown, J. L. & Orians, G. H. (1970). Spacing patterns in mobile animals. *Ann. Rev. Ecol. Syst.*, **1**, 239–62.

Bryant, J. P., Chapin, F. S. III, & Klein, D. R. (1983). Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos*, **40**, 357–68.

Bryant, J. P., Wieland, G. D., Clausen, T. & Kuropat, P. (1985). Interactions of snowshoe hares and feltleaf willow in Alaska. *Ecology* **66**:1564–1573.

Buechner, H. K. & Dawkins, H. C. (1961). Vegetation change induced by elephants and fire in Murchison Falls National Park, Uganda. *Ecology*, **42**, 752–66.

Buechner, H. K., Morrison, J. A. & Leuthold, W. (1966). Reproduction in Uganda kob with special reference to behaviour. In *Comparative Biology of Reproduction in Mammals*, ed. I. W. Rowlands, Symp. Zool. Soc. London 15:69–88.

Buechner, H. K. & Roth, H. D. (1974). The lek system in Uganda kob antelope. *Am. Zool.*, **14**, 145–62.

Bullock, W. R. (1962). The weight of the African elephant. *Proc. Zool. Soc. Lond.*, **138**, 133–5.

Buss, I. O. (1961). Some observations on food habits and behavior of the African elephant. *J. Wildl. Manage.*, **25**, 131–48.

Buss, I. O. & Estes, J. A. (1971). The functional significance of movements and positions of the pinnae of the African elephant. *J. Mammal.*, **52**, 21–7.

Buss, I. O. & Savidge, J. M. (1966). Change in population number and reproductive rate of elephants in Uganda. *J. Wildl. Manage.*, **30**, 791–809.

Calder, W. A. III (1984). *Size, Function and Life History.* Cambridge, Mass.: Harvard University Press. 431pp.

Caughley, G. (1970). Eruption of ungulate populations, with emphasis on Himalayan thar in New Zealand. *Ecology*, **51**, 53–72.

Caughley, G. (1976a). Plant-herbivore systems. In *Theoretical Ecology. Principles and Applications*, ed. R. M. May, pp. 94–113. Oxford: Blackwell.

Caughley, G. (1976b). Wildlife management and the dynamics of ungulate populations. In *Applied Biology*, vol. 1, ed. T. H. Coaker, pp. 183–246. London: Academic Press.

Caughley, G. (1976c). The elephant problem – an alternative hypothesis. *E. Afr. Wildl. J.*, **14**, 265–83.

Caughley, G. (1977). *Analysis of Vertebrate Populations.* New York: Wiley. 234pp.

Caughley, G. (1981). Overpopulation. In *Problems in Management of Locally Abundant Mammals*, ed. P. A. Jewell, S. Holt & D. Hart, pp. 7–20. New York: Academic Press.

Caughley, G. & Goddard, J. (1975). Abundance and distribution of elephants in the Luangwa Valley, Zambia. *E. Afr. Wildl. J.*, **13**, 39–48.

Caughley, G. & Krebs, C. J. (1983). Are big mammals simply small mammals writ large? *Oecologia*, **59**, 7–17.

Cave, A. J. E. (1962). Burchell's original specimens of *Rhinoceros simus. Proc. Zool. Soc. London.*, **139**, 691–700.

Cave, A. J. E., & Allbrook, D. B. (1958). Epidermal structures in a rhinoceros *Cerototherium simum. Nature*, **182**, 196–7.

Chacon, E. & Stobbs, T. H. (1976). Influence of progressive defoliation of a grass sward on the eating behaviour of cattle. *Austr. J. Agric. Res.*, **27**, 709–27.

Chalmers, G. (1963). Breeding data: steinbok. *E. Afr. Wildl. J.*, **1**, 121–2.

Child, G. (1972). Observations on a wildebeest die-off in Botswana. *Arnoldia* (*Rhodesia*), **5**, 31, 1–13.

Child, G., Roth, H. H. & Kerr, M. (1968). Reproduction and recruitment patterns in warthog populations. *Mammalia*, **32**, 6–29.

Churcher, C. S. (1978). Giraffidae. In *Evolution of African Mammals*, ed. V. J. Maglio & H. B. S. Cooke, pp. 509–32. Cambridge, Mass: Harvard University Press.

Cifelli, R. L. (1981). Patterns of evolution among the Artiodactyla and Perissodactyla (Mammalia). *Evol.*, **35**, 433–40.

Clemens, E. T. & Maloiy, G. M. (1982). The digestive physiology of three East African herbivores: the elephant, rhinoceros and hippopotamus. *J. Zool. Lond.*, **198**, 141–56.

Clough, G. (1969). Some preliminary observations on reproduction in the warthog. *J. Reprod. Fert. Suppl.*, **6**, 323–37.

Clough, G. & Hassam, A. G. (1970). A quantitative study of the daily activity of the warthog in the Queen Elizabeth National Park, Uganda. *E. Afr. Wildl. J.*, **8**, 19–24.

Clutton-Brock, T. H. (1984). Reproductive effort and terminal investment in iteroparous animals. *Am. Nat.*, **123**, 212–29.

Clutton-Brock, T. H. & Albon, S. D. (1982). Parental investment in male and female offspring in mammals. In *Current Problems in Sociobiology*, ed. Kings College Sociobiology Group, pp. 223–48. Cambridge: Cambridge University Press.

Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. (1981). Parental investment in male and female offspring in polygynous mammals. *Nature*, **289**, 487–9.

Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. (1984). Maternal dominance, breeding success and birth sex ratios in red deer. *Nature*, **308**, 358–60.

Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. (1985). Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature*, **313**, 131–3.

Clutton-Brock, T. H., Guinness, F. E. & Albon, S. D. (1982). *Red Deer. Behaviour and Ecology of the Two Sexes.* University of Chicago Press, Chicago. 378pp.

Clutton-Brock, T. H. & Harvey, P. H. (1977a). Primate ecology and social organization, *J. Zool. Lond.*, **183**, 1–39.

Clutton-Brock, T. H. & Harvey, P. H. (1977b). Species differences in feeding and ranging behaviour in primates. In *Primate Ecology*, ed. T. H. Clutton-Brock, pp. 557–84. London: Academic Press.

Clutton-Brock, T. H., Harvey, P. H. & Rudder, B. (1977). Sexual dimorphism, socionomic sex ratio and body weight in primates. *Nature*, **269**, 797–800.

Coe, M. J. (1972). Defaecation by African elephants. *E. Afr. Wildl. J.*, **10**, 165–74.

Coe, M. J., Cumming, D. H. M. & Phillipson, J. (1976). Biomass and production of large African herbivores in relation to rainfall and primary production. *Oecologia*, **22**, 341–54.

Coetzee, B. J., Engelbrecht, A. H., Joubert, S. P. J. & Retief; P. F. (1979). Elephant impact on *Sclerocarya* trees in *Acacia nigrescens* tropical plains thornveld of the Kruger National Park. *Koedoe*, **22**, 39–60.

Colbert, E. H. (1969). *Evolution of the Vertebrates.* 2nd edn. New York: John Wiley, 479pp.

Condy, P. R. (1973). The population status, social behaviour and daily activity pattern of the white rhinoceros in Kyle National Park, Rhodesia. M.Sc. thesis, University of Rhodesia.

Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs. *Science*, **199**, 1302–10.

Conybeare, A. (1980). Buffalo numbers, home range and movement in the Sengwa Wildlife Research Area, Zimbabwe. *S. Afr. J. Wildl. Res.*, **10**, 89–93.

Cooper, S. M., & Owen-Smith, N. (1986). Effects of plant spinescence on large mammalian herbivores. *Oecologia*, **68**, 446–55.

Coppens, Y., Maglio, V. J., Madden, C.T. & Beden, M. (1978). Proboscidea. In *Evolution of African Mammals*, ed. V. J. Maglio & H. B. S. Cooke, pp. 336–66. Cambridge, Mass: Harvard University Press.

Corfield, T. F. (1973). Elephant mortality in Tsavo National Park, Kenya. *E. Afr. Wildl. J.*, **11**, 339–68.

Coryndon, S. C. (1978). Hippopotamidae. In *Evolution of African Mammals*, ed. V. J. Maglio & H. B. S. Cooke, pp. 483–96. Cambridge, Mass: Harvard University Press.

Craig, G. C. (1984). Foetal mass and date of conception in African elephants: a revised formula. *S. Afr. J. Sci.*, **80**, 512–16.

Craighead, J. J., Craighead, F. C., Ruff, R. L. & O'Gara, B. W. (1973). Home ranges and activity patterns of non-migratory elk of the Madison Drainage herd as determined by biotelemetry. *Wildl. Monogr.*, **33**, 1–50.

Crook, J. H. & Goss-Custard, J. (1972). Social ethology. *Ann. Rev. Psychol.*, **23**, 277–312.

Croze, H. (1972). A modified photogrammetric technique for assessing age structure of elephant populations and its use in Kidepo National Park. *E. Afr. Wildl. J.*, **10**, 91–115.

Croze, H. (1974a). The Seronera bull problem. I The elephants. *E. Afr. Wildl. J.*, **12**, 1–28.

Croze, H. (1974b). The Seronera bull problem. II The trees. *E. Afr. Wildl. J.*, **12**, 29–47.

Croze, H., Hillman, A. K. K. & Lang, E. (1981). Elephants and their habitats: how do they tolerate each other. In *Dynamics of Large Mammal Populations*, ed. C. W. Fowler & T. D. Smith, pp. 297–316. New York: Wiley.

Cumming, D. H. M. (1975). *A Field Study of the Ecology and Behaviour of Warthog.* Museum Memoir No. 7, pp. 1–179. Salisbury; Trustees of the National Museums and Monuments of Rhodesia.

Cumming, D. H. M. (1981a). The management of elephant and other large mammals in Zimbabwe. In *Management of Locally Abundant Wild Mammals*, ed. P. A. Jewell, S. Holt & D. Hart, pp. 91–118. New York: Academic Press.

Cumming, D. H. M. (1981b). Elephant and woodlands in Chizarira National Park, Zimbabwe. In *Problems in Management of Locally Abundant Wild Mammals*, ed. P. A. Jewell, S. Holt & D. Hart, pp. 347–9. New York: Academic Press.

Cumming, D. H. M. (1982). The influence of large herbivores on savanna structure in Africa. In *The Ecology of Tropical Savannas*, ed. B. J. Huntley & B. H. Walker, pp. 217–45. Berlin: Springer–Verlag.

Cumming, D. H. M. (1983). The decision-making framework with regard to the culling of large mammals in Zimbabwe. In *Management of Large Mammals in African Conservation Areas*, ed. R. N. Owen-Smith, pp. 173–86. Pretoria: Haum.

Cumming, D. H. M., & Jackson, P. (eds.). (1984). *The Status and Conservation of Africa's Elephants and Rhinos.* IUCN, Gland, Switzerland, 191pp.

Dagg, A. I. & Foster, J. B. (1976). *The Giraffe. Its Biology, Behavior and Ecology.* New York: Van Nostrand Reinhold.

Damuth, J. (1981a). Population density and body size in mammals. *Nature*, **290**, 699–700.

Damuth, J. (1981b). Home range, home range overlap and energy use among animals. *Biol. J. Linn. Soc.*, **15**, 185–93.

Darling, F. F. (1937). *A Herd of Red Deer. A Study in Animal Behaviour.* London: Oxford University Press.

Darwin, C. (1871). *The Descent of Man, and Selection in Relation to Sex.* New York: Appleton. 374pp.

David, J. H. M. (1973). The behaviour of bontebok with special reference to territorial behaviour. *Z. Tierpsychol.*, **33**, 38–107.

David, J. H. M. (1978). Observations on territorial behaviour of springbok in the Bontebok National Park, Swellendam. *Zoologica Africana*, **13**, 123–41.

Davis, S. (1985). Tiny elephants and giant mice. *New Scientist*, 3 Jan., 25–7.

Demment, M. W. (1982). The scaling of ruminoreticulum size with body weight in East African ungulates. *Afr. J. Ecol.*, **20**, 43–8.

Demment, M. W. & Van Soest, P. J. (1985). A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *Am. Nat.*, **125**, 641–72.

de Vos, A. & Dowsett, R. J. (1966). The behaviour and population structure of three species of the genus *Kobus*. *Mammalia*, **30**, 30–55.

de Vos, V., Bengis, R. C. & Coetzee, H. J. (1983). In *Management of Large Mammals in African Conservation Areas*, ed. R. N. Owen-Smith, pp. 213–32. Pretoria: Haum.

Dittrich, L. (1972). Gestation periods and age of sexual maturity of some African antelopes. *Int. Zoo Yrb.*, **12**, 184–7.

Dittrich, L. (1976). Age of sexual maturity in the hippopotamus. *Int. Zoo Yrb.*, **16**, 171–3.

Doney, J. M., Ryder, M. L., Gunn, R. G. & Grubb, P. (1974). Colour, conformation, affinities, fleece and patterns of inheritance in Soay sheep. In *Island Survivors*, ed. P. A. Jewell, C. Milner & J. Morton Boyd, pp. 88–125. London: Athlone Press.

Dougall, H. W. & Sheldrick, D. L. W. (1964). The chemical composition of a day's diet of an elephant. *E. Afr. Wildl. J.*, **2**, 51–9.

Douglas-Hamilton, I. (1971). Radio-tracking of elephants. In *Proceedings of a Symposium of Biotelemetry*, pp. 335–342. Pretoria: CSIR.

Douglas-Hamilton, I. (1972). On the ecology and behaviour of the African elephant. PhD thesis, Oxford University.

Douglas-Hamilton, I. (1987). African elephant population trends and their causes. *Oryx*, **21**, 11–14.

Downing, B. H. (1972). A plant ecological survey of the Umfolozi Game Reserve, Zululand. PhD thesis, University of Natal.

Downing, B. H. (1979). Grass protein content and soils as factors affecting area selective grazing by wild herbivores in the Umfolozi Game Reserve, Zululand. *Proc. Grassl. Soc. Sth. Afr.*, **14**, 85–8.

Dowsett, R. J. (1966). Behaviour and population structure of hartebeest in the Kafue National Park. *Puku*, **4**, 147–54.

Dublin, H. (1984). The Serengeti-Mara ecosystem. *Swara*, **7**, 8–13.

Duckworth, B. J. (1972). The distribution and movement of buffalo herds in the Kalahari sand area of Wankie National Park. Certif. in Field Ecol. thesis, University of Rhodesia.

Dunbar, R. I. M. (1979). Energetics, thermoregulation and the behavioural ecology of the klipspringer. *Afr. J. Ecol.*, **17**, 217–30.

Dunbar, R. I. M. & Dunbar, E. P. (1974). Social organization and ecology of the klipspringer in Ethiopia. *Z. Tierpsychol.*, **35**, 481–93.

Duncan, P. (1975). Topi and their food supply. PhD thesis, University of Nairobi.

Duncan, P. (1980). Time budgets of Camargue horses. II Time-budgets of adult horses and weaned subadults. *Behaviour*, **72**, 26–49.

Dunham, K. M. (1982). The foraging behaviour of impala. *S. Afr. J. Wildl. Res.*, **12**, 36–40.

Dunham, K. M. (1986). Movements of elephant cows in the unflooded Middle Zambezi Valley, Zimbabwe, *Afr. J. Ecol.*, **24**, 287–91.

du Plessis, S. S. (1969). The past and present geographical distribution of the Perissodactyla and Artiodactyla in Southern Africa. MSc. thesis, University of Pretoria.

du Plessis, S. S. (1972). Ecology of blesbok with special reference to productivity. *Wildl. Monogr.*, **30**, 1–70.

du Preez. J. S. & Grobler, J. D. (1977). Drinking times and behaviour at waterholes of some game species in Etosha National Park. *Madoqua*, **10**, 61–70.

Du Toit, P. J., Louw, J. G. & Malan, A. J. (1940). A study of the mineral content and feeding value of the natural pastures in the Union of South Africa. *Onderstepoort J. Vet. Sci.*, **14**, 123–327.

Dye, P. J. (1983). Prediction of variation in grass growth in a semi-arid induced grassland. PhD thesis, University of the Witwatersrand.

East, R. (1981). Species area curves and populations of large mammals in African savanna reserves. *Biol. Cons.*, **21**, 111–26.

East, R. (1984). Rainfall, soil nutrient status and biomass of large African savanna animals. *Afr. J. Ecol.*, **22**, 245–70.

Eisenberg, J. F. & Lockhart, M. (1972). *An Ecological Reconnaissance of Wilpattu National Park, Ceylon.* Smithsonian Contributions to Zoology No. 101, Washington D.C.: Smithsonian Institution Press.

Eisenberg, J. F., McKay, G. M. & Jainudeen, M. R. (1971). Reproductive behaviour of the Asiatic elephant. *Behaviour*, **38**, 193–225.

Eisenberg, J. F. & Seidensticker, J. (1976). Ungulates in southern Asia. A consideration of biomass estimates for selected habitats. *Biol. Cons.*, **10**, 293–308.

Ellerman, J. R., Morrison-Scott, T. S. C. & Hayman A. W. (1953). *South African Mammals 1758–1951.* London: British Museum (Nat. Hist.) Trustees.

Eltringham, S. K. (1974). Changes in the large mammal community of Mweya Peninsula, Rwenzori National Park, following removal of hippopotamus. *J. Appl. Ecol.*, **11**, 855–65.

Eltringham, S. K. (1977). The numbers and distribution of elephant in the Rwenzori National Park and Chambura Game Reserve, Uganda. *E. Afr. Wildl. J.*, **15**, 19–39.

Eltringham, S. K. (1980). A quantitative assessment of range usage by large African mammals with particular reference to the effect of elephants on trees. *Afr. J. Ecol.*, **18**, 53–71.

Eltringham, S. K. (1982). *Elephants*. Poole, Dorset: Blandford Books.

Eltringham, S. K. & Din, N. A. (1977). Estimates of the population size of some ungulate species in the Rwenzori National Park, Uganda. *E. Afr. Wildl. J.*, **15**, 305–16.

Eltringham, S. K. & Woodford, M. H. (1973). The numbers and distribution of buffalo in the Rwenzori National Park, Uganda. *E. Afr. Wildl. J.*, **11**, 151–64.

Emlen, S. T. & Oring, L. W. (1977). Ecology, sexual selection and the evolution of mating systems. *Science*, **197**, 215–23.

Estes, R. D. (1966). Behaviour and life history of the wildebeest. *Nature*, **212**, 999–1000.

Estes, R. D. (1967). The comparative behavior of Grant's and Thomson's gazelles. *J. Mammal.*, **48**, 189–209.

Estes, R. D. (1974). Social organization of the African bovids. In *The Behaviour of Ungulates and its Relation to Management*, ed. V. Geist & F. Walther, pp. 166–205. IUCN public new series no. 24, Morges: IUCN.

Estes, R. D. (1976). The significance of breeding synchrony in the wildebeest. *E. Afr. Wildl. J.*, **14**, 135–52.

Estes, R. D. & Estes, R. K. (1974). The biology and conservation of the giant sable antelope, *Proc. Acad. Nat. Sci. Philadelphia*, **126**, 73–104.

Farentinos, R. C. (1972). Social dominance and mating activity in the tassle-eared squirrel. *Anim. Behav.*, **20**, 316–26.

Fenchel, T. (1974). Intrinsic rate of natural increase: the relationship with body size. *Oecologia*, **14**, 317–26.

Ferrar, A. A. (1983). *Handbook for the Management of African Large Mammals*. Pretoria: CSIR.

Field, C. R. (1970). A study of the feeding habits of hippopotamus in the Queen Elizabeth National Park, Uganda, with management implications. *Zoologica Africana*, **5**, 71–86.

Field, C. R. (1971). Elephant ecology in the Queen Elizabeth National Park, Uganda. *E. Afr. Wildl. J.*, **9**, 99–123.

Field, C. R. & Blankenship, L. H. (1973). Nutrition and reproduction of Grant's and Thomson's gazelles, Coke's hartebeest and giraffe in Kenya. *J. Reprod. Fert. Suppl*, **19**, 287–301.

Field, C. R. & Laws, R. M. (1970). The distribution of the larger herbivores in the Queen Elizabeth National Park, Uganda. *J. Appl. Ecol.*, **7**, 273–94.

Field, C. R. & Ross, I.C. (1976). The savanna ecology of Kidepo Valley National Park. II Feeding ecology of elephant and giraffe. *E. Afr. Wildl. J.*, **14**, 1–16.

Finch, V. A. (1972). Thermoregulation and heat balance of the East African eland and hartebeest. *Am. J. Phys.*, **222**, 1374–9.

Fisher, D. C. (1984). Mastodon butchery by North American Paleo-Indians. *Nature*, **308**, 271–2.

Fisher, R. A. (1930). *The Genetical Theory of Natural Selection*. Oxford: Oxford University Press. 291pp.

Floody, O. R. & Arnold, A. P. (1975). Uganda kob: territoriality and the spatial distributions of sexual and agonistic behaviors at a territorial ground. *Z. Tierpsychol.*, **37**, 192–212.

Foose, T. J. (1982). Trophic strategies of ruminant vs nonruminant ungulates. PhD thesis, University of Chicago.

Fortelius, M. (1982). Ecological aspects of the dental functional morphology of the Plio-Pleistocene rhinoceroses of Europe. In *Teeth: Form, Function and Evolution.* ed. B. Kurten, New York: Columbia University Press.

Foster, J. B. (1967). The square-lipped rhino. *E. Afr. Wildl. J.*, **5**, 167–70.

Foster, J. B. & Coe, M. J. (1968). The biomass of game animals of Nairobi National Park 1960–1966. *J. Zool. Lond.*, **155**, 413–28.

Foster, J. B. & Dagg, A. I. (1972). Notes on the biology of the giraffe. *E. Afr. Wildl. J.*, **10**, 1–16.

Fowler, C. W. (1981). Density dependence as related to life history strategy. *Ecology*, **62**, 602–10.

Frame, G. W. (1971). The black rhinoceros. *Animals*, **13**, 693–9.

Frame, G. W. (1980). Black rhinoceros sub-population on the Serengeti Plains, Tanzania. *Afr. J. Ecol.*, **18**, 155–66.

Frame, G. W. & Goddard, J. (1970). Black rhinoceros vocalizations. *E. Afr. Wildl. J.*, **8**, 207.

Gadgil, M. (1971). Dispersal: population consequences and evolution. *Ecology*, **52**, 253–61.

Gaines, M. S. & McLenaghan, L. R. Jr. (1980). Dispersal in small mammals. *Ann. Rev. Ecol. Syst.*, **11**, 163–96.

Garland, T., Jr. (1983). Scaling the ecological cost of transport to body mass in terrestrial mammals. *Am. Nat.*, **121**, 571–87.

Geist, V. (1966). The evolution of horn-like organs. *Behaviour*, **27**, 175–214.

Geist, V. (1971). *Mountain Sheep: A Study in Behavior and Evolution.* Chicago: University of Chicago Press. 383pp.

Geist, V. (1974a). On the relationship of social evolution and ecology in ungulates. *Am. Zool.*, **14**, 205–220.

Geist, V. (1974b). On the relationship of ecology and behaviour in the evolution of ungulates: theoretical considerations. In *The Behaviour of Ungulates and its Relation to Management*, ed. V. Geist & F. R. Walther, pp. 235–46. IUCN public, new series no. 24, Morges: IUCN.

Geist, V. (1981). On the reproductive strategies in ungulates and some problems of adaptation. In *Evolution Today*, ed. G. G. E. Scudder & J. L. Reveal, Proc. 2nd Int. Cong. Syst. Biol., pp. 111–32.

Geist, V. & Bayer, M. (1988). Sexual dimorphism in the Cervidae and its relation to habitat, *J. Zool., Lond.*, **214**, 45–53.

Georgiadis, N. (1985). Growth patterns, sexual dimorphism and reproduction in African ruminants. *Afr. J. Ecol.*, **23**, 75–88.

Getz, L. L. (1972). Social structure and aggressive behavior in a population of *Microtus pennsylvanicus*. *J. Mammal.*, **53**, 310–17.

Gilbert, B. M. & Martin, L. D. (1984). Late Pleistocene fossils of Natural Trap Cave, Wyoming, and the climatic model of extinction. In *Quaternary Extinctions*, ed. P. S. Martin & R. G. Klein, pp. 138–147. Tucson: University of Arizona Press.

Gingerich, P. G. (1984). Pleistocene extinctions in the context of origination-extinction equilibria in Cenozoic mammals. In *Quaternary Extinctions*, ed. P. S. Martin & R. G. Klein, pp. 211–22. Tucson: University of Arizona Press.

Glover, J. (1963). The elephant problem at Tsavo. *E. Afr. Wildl. J.*, **1**, 30–9.

Goddard, J. (1966). Mating and courtship of the black rhinoceros. *E. Afr. Wildl. J.*, **4**, 69–76.

Goddard, J. (1967). Home range behaviour and recruitment rates of two black rhinoceros populations. *E. Afr. Wildl. J.*, **5**, 133–50.

Goddard, J. (1968). Food preferences of two black rhinoceros populations. *E. Afr. Wildl. J.*, **6**, 1–18.

Goddard, J. (1969). Aerial census of black rhinoceros using stratified random sampling. *E. Afr. Wildl. J.*, **7**, 105–14.

Goddard, J. (1970a). Age criteria and vital statistics of a black rhinoceros population. *E. Afr. Wildl. J.*, **8**, 105–21.

Goddard, J. (1970b). A note on age at sexual maturity in wild black rhinoceros. *E. Afr. Wildl. J.*, **8**, 208.

Gogan, P. J. P. (1973). Some aspects of nutrient utilization by Burchell's zebra in the Serengeti-Mara region, East Africa. MSc thesis, Texas A&M University.

Gold, A. (1973). Energy expenditure in animal locomotion. *Science*, **181**, 275–6.

Goodman, D. (1981). Life history analysis of large mammals. In *Dynamics of Large Mammal Populations*, ed. C. W. Fowler & T. D. Smith, pp. 415–436. New York: Wiley.

Gosling, L. M. (1974). The social organization of Coke's hartebeest. In *The Behaviour of Ungulates and Its Relation to Management*, ed. V. Geist & F. R. Walther, pp. 488–511. IUCN public, new series no. 24, Morges: IUCN.

Gould, S. J. & Vrba, E. S. (1982). Exaptation – a missing term in the science of form. *Paleobiology*, **8**, 4–15.

Graham, R. W. & Lundelius, E. L. (1984). Coevolutionary disequilibrium and Pleistocene extinctions. In *Quaternary Extinctions*, ed. P. S. Martin & R. G. Klein, pp. 223–49. Tucson: University of Arizona Press.

Grayson, D. K. (1977). Pleistocene avifaunas and the overkill hypothesis. *Science*, **195**, 691–3.

Greer, K. R. & Howe, R. E. (1964). Winter weights of northern Yellowstone elk. *Trans. N. Am. Wildl. Conf.*, **29**, 237–48..

Grimsdell, J. J. R. & Field, C. R. (1976). Grazing patterns of buffalos in the Rwenzori National Park, Uganda. *E. Afr. Wildl. J.*, **14**, 339–44.

Grobler, J. H. (1973). Biological data on tsessebe in Rhodesia. *Arnoldia* (*Rhodesia*), **6**, 12, 1–16.

Grobler, J. H. (1974). Aspects of the biology, population ecology and behaviour of the sable in the Rhodes Matopos National Park, Rhodesia. *Arnoldia* (*Rhodesia*), **7**, 6, 1–36.

Grobler, J. H. (1980). Breeding behaviour and aspects of social behaviour of sable in the Rhodes Matopos National Park, Zimbabwe. *S. Afr. J Wildl. Res.*, **10**, 150–2.

Groves, C. P. (1967). Geographic variation in the black rhinoceros. *Z. Saugetierk*, **32**, 267–76.

Groves, C. P. & Kurt, F. (1972). *Dicerorhinus sumatrensis. Mammalian species No. 21.* American Soc. of Mammalogists. 6pp.

Grubb, P. (1974). Mating activity and the social significance of rams in a feral sheep community. In *The Behaviour of Ungulates and its Relation to Management*, ed. V. Geist & F. Walther, pp. 457–76. IUCN public, new series no. 24, Morges: IUCN.

Grubb, P. and Jewell, P. A. (1974). Movement, daily activity and home range of Soay sheep. In *Island Survivors*, ed. P. A. Jewell, C. Milner & J. Morton Boyd, pp. 160–194. London: Athlone Press.

Gruhn, R. & Bryan, A. L. (1984). The record of Pleistocene megafaunal extinctions at Taima-taima, northern Venezuela. In *Quaternary Extinctions*, ed. P. S. Martin & R. G. Klein, pp. 128–37. Tucson, Arizona: University of Arizona Press.

Grunow, J. O., Groeneveld, H. T. & du Toit, H. C. (1980). Above ground dry matter dynamics of the grass layer in the Nylsvley tree savanna. *J. Ecol.*, **68**, 877–84.

Guggisberg, C. A. W. (1961). *Simba. The Life of the Lion.* London: Andre Deutch.

Guggisberg, C. A. W. (1966). *S.O.S. Rhino.* London: Andre Deutsch. 174pp.

Guidon, N. & Delibrias, G. (1986). Carbon-14 dates point to man in the Americas 32,000 years ago. *Nature*, **321**, 769–72.

Guilday, J. E. (1984). Pleistocene extinction and environmental change: case study of the Appalachians. In *Quaternary Extinctions*, ed. P. S. Martin & R. G. Klein, pp. 250–8. Tucson: University of Arizona Press.

Guthrie, R. D. (1982). Mammals of the mammoth steppe as paleoenvironmental indicators. In *Paleoecology of Beringia*, ed. D. M. Hopkins, J. V. Matthews, C. E. Schweger & S. B. Young, pp. 307–26. New York: Academic Press.

Guthrie, R. D. (1984). Mosaics, allelochemics and nutrients. An ecological theory of late Pleistocene megafaunal extinctions. In *Quaternary Extinctions*, ed. P. S. Martin & R. G. Klein, pp. 259–98. Tucson: University of Arizona Press.

Guy, P. (1974). Feeding behaviour of the African elephant in the Sengwa Research Area of Rhodesia. MSc thesis, University of Rhodesia.

Guy, P. R. (1975). The daily food intake of the African elephant. *Arnoldia (Rhodesia)*, **7**, 26, 1–6.

Guy, P. R. (1976a). The feeding behaviour of elephant in the Sengwa Area, Rhodesia. *S. Afr. J. Wildl. Res.*, **6**, 55–64.

Guy, P. R. (1976b). Diurnal activity patterns of elephant in the Sengwa area, Rhodesia, *E. Afr. Wildl. J.*, **14**. 285–95.

Guy, P. R. (1981). Changes in the biomass and productivity of woodlands in the Sengwa Research Area, Zimbabwe, *J. Appl. Ecol.*, **18**, 507–19.

Hall-Martin, A. J. (1974). Food selection by Transvaal lowveld giraffe as determined by analysis of stomach contents. *J. Sth. Afr. Wildl. Mgmt. Ass.*, **4**, 191–202.

Hall-Martin, A. J. (1975). Aspects of the ecology and sociality of the giraffe. *Die Soogdiernavorsingsinstituut 1966–1975*, pp. 48–56. Pretoria: University of Pretoria.

Hall-Martin, A. J. (1980). Elephant survivors. *Oryx*, **15**, 355–62.

Hall-Martin, A. J. (1984). Conservation and management of elephants in the Kruger National Park, South Africa. In *The Status and Conservation of Africa's Elephants and Rhinos*, ed. D. H. M. Cumming & P. Jackson, pp. 104–18. Gland: IUCN.

Hall-Martin, A. J. (1985). The nabab of Aukoerebis. *African Wildlife*, **39**, 244–7.

Hall-Martin, A. J. (1986). Recruitment in a small black rhino population. *Pachyderm*, **7**, 6–8.

Hall-Martin, A. J. (1987). Kruger's magnificent seven still capture the imagination. *Custos*, **16**, 26–8.

Hall-Martin, A. J. & Basson, W. D. (1975). Seasonal chemical composition of the diet of Transvaal lowveld giraffe. *J. Sth. Afr. Wildl. Mgmt. Ass.*, **5**, 19–21.

Hall-Martin, A. J., Erasmus, T. & Botha, B. P. (1982). Seasonal variation of diet and faeces composition of black rhinoceros in the Addo Elephant National Park. *Koedoe*, **25**, 63–82.

Hall-Martin, A. J. & Penzhorn, B. L. (1977). Behaviour and recruitment of translocated black rhinoceros. *Koedoe*, **20**, 147–62.

Hall-Martin, A. J. & Skinner, J. D. (1978). Observations on puberty and pregnancy in female giraffe. *J. Sth. Afr. Wildl. Mgmt. Ass.*, **8**, 91–4.

Hall-Martin, A. J., Skinner, J. D. & Smith, A. (1977). Observations on lactation and milk composition of the giraffe. *S. Afr. J. Wildl. Res.*, **7**, 67–71.

Hall-Martin, A. J., Skinner, J. D. & Van Dyk, J. M. (1975). Reproduction in the giraffe in relation to some environmental factors. *E. Afr. Wildl. J.*, **13**, 237–45.

Hamilton, W. D. & May, R. M. (1977). Dispersal in stable habitats. *Nature*, **269**, 578–81.

Hanks, J. (1969a). Growth in weight of the female African elephant in Zambia. *E. Afr. Wildl. J*, **7**, 7–10.

Hanks, J. (1969b). Seasonal breeding of the African elephant in Zambia. *E. Afr. Wildl. J.*, **7**, 167.

Hanks, J. (1972a). Growth of the African elephant. *E. Afr. Wildl. J.*, **10**, 251–272.

Hanks, J. (1972b). Reproduction of elephant in the Luangwa Valley, Zambia. *J. Reprod. Fert.*, **30**, 13–26.

Hanks, J. (1973). Reproduction in the male African elephant in the Luangwa Valley, Zambia, *J. Sth. Afr. Wildl. Mgmt. Ass.*, **3**, 31–9.

Hanks, J. (1979). *A Struggle for Survival.* Cape Town: Struik.

Hanks, J. & McIntosh, E. A. (1973). Population dynamics of the African elephant. *J. Zool., Lond.*, **169**, 29–38.

Harestad, A. S. & Bunnell, F. L. (1979). Home range and body weight – a reevaluation. *Ecology*, **60**, 389–402.

Harrington, G. N. & Ross, I. C. (1974). The savanna ecology of Kidepo Valley National Park. I The effects of burning and browsing on the vegetation. *E. Afr. Wildl. J.*, **12**, 93–106.

Harris, W. C. (1838). *Narrative of an Expedition into Southern Africa During the Years 1836 and 1837.* London: John Murray.

Harvey, P. H. & Clutton-Brock, T. H. (1981). Primate home range size and metabolic needs. *Behav. Ecol. Sociobiol.*, **8**, 151–5.

Hatton, J. C. & Smart, N. O. E. (1984). The effect of long term exclusion of large herbivores on soil nutrient status in Murchison Falls National Park, Uganda. *Afr. J. Ecol.*, **22** 23–30.

Hawkins, R. E., Klimstra, W. D. & Autry, D. C. (1971). Dispersal of deer from Crab Orchard National Wildlife Refuge. *J. Wildl. Manage.*, **35**, 216–20.

Haynes, C. V. (1982). Were Clovis pregenitors in Beringia? In *Paleoecology of Beringia*, ed. D. M. Hopkins, J. V. Matthews, C. E. Schweger & S. B. Young, pp. 383–98. New York: Academic Press.

Heller, E. (1913). The white rhinoceros. *Smithsonian Miscellaneous Collections* **61**, 1–77.

Hendrichs, H. (1971). Freilandsbeobachtungen zum Sozialsystem der Afrikanischen Elefanten. In *Dikdik und Elefanten*, ed. H. Hendrichs, pp. 77–173. Munich: R. Piper Verlag.

Hendrichs, H. (1975). Changes in a population of dikdik. *Z. Tierpsychol.*, **38**, 55–69.

Hendrichs, H. & Hendrichs, U. (1971). Freilandsuntersuchunen zur Okologie und Ethologie der Zwerg-Antilope *Madoqua (Rhynchotragus) kirki* Gunther 1880. In *Dikdik und Elefanten*, ed. H. Hendrichs, pp. 9–73. Munich: R. Piper Verlag.

Hennemann, W. W. III. (1983). Relationship among body mass, metabolic rate and the intrinsic rate of natural increase in mammals. *Oecologia*, **56**, 104–8.

Hillman, J. C. (1979). The biology of eland in the wild. PhD thesis, University of Nairobi.

Hillman-Smith, A. K. K., Owen-Smith, N., Anderson, J. L., Hall-Martin, A. J. & Selaladi, J. P. (1986). Age estimation of the white rhinoceros. *J. Zool. Lond.*, **210**, 355–79.

Hillman-Smith, A. K. K., Oyisenzoo, K. M. & Smith, F. (1986). A last chance to save the northern white rhino? *Oryx*, **20**, 20–6.

Hintz, H. F., Schryver, H. F. & Stevens, C. E. (1978). Digestion and absorption in the hindgut of nonruminant herbivores. *J. Anim. Sci.*, **46**, 1803–7.

Hirst, S. M. (1975). Ungulate–habitat relationships in a South African savanna. *Wildl. Monogr.* No. 44, 60pp.

Hitchins, P. M. (1968). Liveweights of some mammals from Hluhluwe Game Reserve, Zululand. *Lammergeyer* (*Natal*), **9**, 42.

Hitchins, P. M. (1971). Preliminary findings in a radiotelemetric study on the black rhinoceros in Hluhluwe Game Reserve, Zululand. *Symposium in Biotelemetry*, Pretoria, 1971, pp. 79–100. Pretoria: CSIR.

Hitchins, P. M. (1979). The effects of the black rhinoceros on the vegetation of the NE area of Hluhluwe Game Reserve. Mimeog. paper presented at the Symposium/Workshop on the Vegetation Dynamics of the Hluhluwe-Corridor-Umfolozi Complex, 10–12 August 1979, 7 pp. Natal Parks Board.

Hitchins, P. M., & Anderson, J. L. (1983). Reproductive characteristics and management of the black rhinoceros in the Hluhluwe/Corridor/Umfolozi Game Reserve Complex, *S. Afr. J. Wildl. Res.*, **13**, 78–85.

Hitchins, P. M. & Vincent, J. (1972). Observations on range extension and dispersal of impala in Zululand. *J. Sth. Afr. Wildl. Mgmt Ass.*, **2**, 3–8.

Hofmann, R. R. (1973). *The Ruminant Stomach.* East Afr. Monogr. Biol. Vol. 2. Nairobi: East African Literature Bureau.

Hofmann, R. R. & Stewart, D. R. M. (1972). Grazer or browser: a classification based on the stomach structure and feeding habits of East African ruminants. *Mammalia*, **36**, 226–40.

Holling, C. S. (1965). The functional response of predators to prey density and its role in mimicry and population regulation. *Mem. Entomol. Soc. Can.*, **45**, 1–60.

Hoogerwerf, A. (1970). *Udjong Kulon. Land of the Last Javan Rhinoceros.* Leiden: E. J. Brill.

Hooijer, D. A. (1969). Pleistocene East African rhinoceroses. In *Fossil Vertebrates of Africa*, ed. L. B. Leakey, vol. 1, pp. 71–98. London: Academic Press.

Hooijer, D. A. (1978). Rhinocerotidae. In *Evolution of African mammals*, ed. V. J. Maglio & H. B. S. Cooke, pp. 371–8. Cambridge, Mass: Harvard University Press.

Hooijer, D. A. & Patterson, B. (1972). Rhinoceroses from the Pliocene of north-western Kenya. *Bull. Mus. Compar. Zool.* (*Harvard Univ.*), **144**, 1–26.

Hope, G. (1984). Australian environmental change: timing, direction, magnitude, and rates. In *Quaternary Extinctions*, ed. P. S. Martin & R. G. Klein, pp. 681–90. Tucson: University of Arizona Press.

Hopkins, D. M. (1982). Aspects of the paleogeography of Beringia during the late Pleistocene. In *Paleoecology of Beringia*, ed. D. M. Hopkins, J. V. Matthews, C. E. Schweger & S. B. Young, pp. 3–28. New York: Academic Press.

Hopkins, D. M., Matthews, J. V., Schweger, C. E. & Young S. B. (eds.) (1982). *Paleoecology of Beringia.* New York: Academic Press.

Hoppe, P. P. (1977a). Comparison of voluntary food and water consumption and digestion in Kirk's dikdik and suni. *E. Afr. Wildl. J.*, **15**, 41–8.

Hoppe, P. P. (1977b). Rumen fermentation and body weight in African ruminants. *Proc. XIIIth Congress of Game Biologists*, pp. 141–50.

Hoppe, P. P., Gwynne, M. D. & van Hoven, W. (1981). Nutrients, protozoa and volatile fatty acids in the rumen of Harvey's red duiker. *S. Afr. J. Wildl. Res.*, **11**, 110–1.

Hoppe, P. P., Qvortrup, S. A. & Woodford, M. H. (1977a). Rumen fermentation and food selection in East African sheep, goats, Thomson's gazelle, Grant's gazelle and impala. *J. Agric. Sci. Camb.*, **89**, 129–35.

Hoppe, P. P., Qvortrup, S. A. & Woodford, M. H. (1977b). Rumen fermentation and food selection in East African zebu cattle, wildebeest, Coke's hartebeest, and topi. *J. Zool. Lond.*, **181**, 1–9.

Horn, H. S. (1978). Optimal tactics of reproduction and life history. In *Behavioural Ecology. An Evolutionary Approach*, ed. J. R. Krebs & N. B. Davies, pp. 411–30. Oxford: Blackwell.

Horton, D. R. (1984). Red kangaroos: last of the Australian megafauna. In *Quaternary Extinctions*, ed. P. S. Martin & R. G. Klein, pp. 639–80. Tucson: University of Arizona Press.

Houston, D. B. (1971). Ecosystems of National Parks. *Science*, **172**, 648–51.

Houston, D. B. (1982). *The Northern Yellowstone Elk. Ecology and Management.* New York: Macmillan. 474pp.

Hubback, T. (1939). The Asiatic two-horned rhinoceros. *J. Mammal.*, **20**, 1–20.

Huntley, B. J. (1967). *Ceratotherium simum* (Burchell). A literature survey. B.Sc. Hons. report, University of Pretoria.

Huntley, B. J. (1971). Seasonal variation in the physical condition of mature male blesbok and kudu. *J. Sth. Afr. Wildl. Mgmt. Ass.*, **1**, 17–19.

Hutchinson, G. E. (1975). Variations on a theme by Robert MacArthur. In *Ecology and Evolution of Communities*, ed. M. L. Cody & J. M. Diamond, pp. 492–521. Cambridge, Mass: Harvard University Press.

Hvidberg-Hansen, H. (1970). Contribution to the knowledge of the reproductive physiology of the Thomson's gazelle. *Mammalia*, **34**, 551–63.

Irby, L. R. (1977). Studies on mountain reedbuck populations with special reference to the Loskop Dam Nature Reserve. *S. Afr. J. Wildl. Res.*, **7**, 73–86.

Irby, L. R. (1981). Mountain reedbuck activity patterns in the Loskop Dam Nature Reserve. *S. Afr. J. Wildl. Res.*, **11**, 115–20.

Ishwaran, R. (1981). Comparative study on elephant populations in Gal Oya, Sri Lanka. *Biol. Cons.*, **21**, 303–13.

Ishwaran, N. (1983). Elephant and woody plant relationships in Gal Oya, Sri Lanka. *Biol. Cons.*, **26**, 255–70.

IUCN (1980). *World Conservation Strategy.* Gland, Switzerland: IUCN.

Jachmann, H. (1980). Population dynamics of the elephants in the Kasungu National Park, Malawi. *Netherlands J. Zool.*, **30**, 622–34.

Jachmann, H. (1985). Estimating age in African elephants. *Afr. J. Ecol.*, **23**, 199–202.

Jachmann, H. (1986). Notes on the population dynamics of the Kasungu elephants. *Afr. J. Ecol.*, **24**, 215–26.

Jachmann, H. & Bell, R. H. V. (1984). Why do elephants destroy woodland? *African Elephant and Rhino Group Newsletter*, **3**, 9–10.

Jachmann, H. & Bell, R. H. V. (1985). Utilization by elephants of the *Brachystegia* woodlands of the Kasungu National Park, Malawi. *Afr. J. Ecol.*, **23**, 245–58.

Jacobsen, N. H. G. (1973). Distribution, home range and behaviour patterns of bushbuck in the Lutope and Sengwa valleys, Rhodesia, *J. Sth. Afr. Wildl. Mgmt. Ass.*, **4**, 75–93.

Jainudeen, M. R., McKay, G. M. & Eisenberg, J. F. (1972). Observations on musth in the domesticated Asian elephant. *Mammalia*, **36**, 247–61.

Janis, C. (1976). The evolutionary strategy of the Equidae and the origins of rumen and caecal digestion. *Evolution*, **30**, 757–76.

Jarman, P. J. (1968). The effect of the creation of Lake Kariba upon the terrestrial ecology of the middle Zambezi valley. PhD thesis, University of Manchester.

Jarman, P. J. (1974). The social organization of antelope in relation to their ecology. *Behaviour*, **48**, 215–67.

Jarman, P. J. & Jarman, M. V. (1973a). Daily activity of impala. *E. Afr. Wildl. J.*, **11**, 75–92.

Jarman, P. J. & Jarman, M. V. (1973b). Social behaviour, population structure and reproductive potential in impala. *E. Afr. Wildl. J.*, **11**, 329–38.

Jarman, P. J. & Jarman, M. V. (1974). A review of impala behaviour and its relevance to management. In *The Behaviour of Ungulates and its Relation to Management*, ed. V. Geist & F. Walther, pp. 871–81. IUCN public, new series no. 24, Morges: IUCN.

Jarman, P. J. & Sinclair, A. R. E. (1979). Feeding strategy and the patterning of resource partitioning in ungulates. In *Serengeti. Dynamics of an Ecosystem*, ed. A. R. E. Sinclair & M. Norton-Griffiths, pp. 130–63. Chicago: University of Chicago Press.

Jewell, P. A. (1966). The concept of home range in mammals. *Symp. Zool. Soc. London*, **18**, 85–109.

Jewell, P. A. (1972). Social organization and movements of topi during the rut at Ishasha, Queen Elizabeth Park, Uganda. *Zoologica Africana*, **7**, 233–55.

Joubert, E. (1970). The taxonomic status of the rhinoceros in South West Africa. *Madoqua* (*South West Africa*), **2**, 27–38.

Joubert, E. (1972). The social organization and associated behaviour in the Hartmann zebra. *Madoqua* (*South West Africa*), **6**, 17–56.

Joubert, E. (1974). Notes on the reproduction in Hartmann zebra in South West Africa. *Madoqua*, **1**, 31–6.

Joubert, E. & Eloff, F. C. (1971). Notes on the ecology and behaviour of the black rhinoceros in South West Africa. *Madoqua* (*South West Africa*), **3**, 5–54.

Joubert, S. C. J. (1972). Territorial behaviour of the tsessebe in the Kruger National Park. *Zoologica Africana*, **7**, 141–56.

Joubert, S. C. J. (1974). The social organization of the roan antelope and its influence on the spatial distribution of herds in the Kruger National Park. In *The Behaviour of Ungulates and its Relation to Management*, ed. V. Geist & F. Walther, pp. 661–675. IUCN public., new series no. 24, Morges: IUCN.

Joubert, S. C. J. (1975). The mating behaviour of the tsessebe. *Z. Tierpsychol.*, **37**, 182–91.

Joubert, S. C. J. (1983). A monitoring programme for an extensive national park. In *Management of Large Mammals in African Conservation Areas*, ed. R.N. Owen-Smith, pp. 201–212. Pretoria: Haum.

Joubert, S. C. J. & Bronkhorst, P. J. L. (1977). Some aspects of the history and population ecology of the tsessebe in the Kruger National Park. *Koedoe*, **20**, 125–45.

Jungius, H. (1971a). Studies on the food and feeding behaviour of the reedbuck in the Kruger National Park. *Koedoe*, **14**, 65–97.

Jungius, H. (1971b). The biology and behaviour of the reedbuck in the Kruger National Park. *Mammalia Depicta*, Berlin: Paul Parey. 106pp.

Keith, L. B. & Wyndberg, L. A. (1978). A demographic analysis of the snowshoe hare cycle. *Wildl. Monogr.* No. 59, 70pp.

Kingdon, J. (1979). *East African Mammals. An Atlas of Evolution in Africa.* vol. III B (Large Mammals). London: Academic Press. 435pp.

Kingdon, J. (1982). *East African Mammals. An Atlas of Evolution in Africa.* vol. III C. Bovids. London: Academic Press.

Kirby, F. V. (1920). The white rhinoceros in Zululand. *Ann. Durban Mus.*, **2**, 223–42.

Kleiber, M. (1961). *The Fire of Life.* New York: John Wiley.

Klein, R. G. (1977). The ecology of early man in southern Africa. *Science*, **197**, 115–26.

Klein, R. G. (1984a). Mammalian extinctions and Stone Age people in Africa. In *Quaternary Extinctions*, ed. P. S. Martin & R. G. Klein, pp. 553–73. New York: Academic Press.

Klein, R. G. (1984b). The large mammals of southern Africa: late Pleistocene to Recent. In *Southern African Prehistory and Paleoenvironments*, ed. R. G. Klein, pp. 107–46. Rotterdam: Balkema.

Klingel, H. (1965). Notes on the biology of the plains zebra. *E. Afr. Wildl. J.*, **3**, 86–8.

Klingel, H. (1967). Soziale Organisation und Verhalten freilebender Steppenzebras. *Z. Tierpsychol.*, **24**, 580–624.

Klingel, H. (1969). Reproduction in the plains zebra, behaviour and ecological factors. *J. Reprod. Fert. Suppl.* **6**, 339–45.

Klingel, H. (1974). Soziale Organization und Verhalten des Grevy-Zebras. *Z. Tierpsychol.*, **36**, 37–70.

Klingel, H. (1975). Das Verhalten der Pferde (Equidae). *Handbuch der Zoologie*, **8**, 10, 65pp.

Klingel, H. & Klingel, U. (1966). Rhinoceroses of Ngorongoro Crater. *Oryx*, **8**, 302–6.

Klös, H.-G. & Frese, R. (1978). Population trends in African rhinoceroses living in zoos and safari parks. *Int. Zoo Yrb.*, **18**, 231–4.

Klös, H.-G. & Frese, R. (1981). *International Studbook of the Black Rhinoceros*, 45pp., and *International Studbook of the White Rhinoceros*, 52pp. Berlin Zoological Garden.

Kok, O. B. (1975). *Behaviour and Ecology of the Red Hartebeest.* Orange Free State Prov. Admin., Nature Cons. Misc. Publ. No. 4.

Kok, O. B. & Opperman, D. P. J. (1980). Voedingsgedrag van kameelperde in die Willem Pretorius Wildtuin, Oranje-Vrystaat. *S. Afr. J. Wildl. Res.*, **10**, 45–55.

Konigkramer, A. J. (1983). Influencing public attitudes: the socio-politics of culling in Natal. In *Management of Large Mammals in African Conservation Areas*, ed. R. N. Owen-Smith, pp. 233–40. Pretoria; Haum.

Kortlandt, A. (1976). Tree destruction by elephants in Tsavo National Park and the role of man in African ecosystems. *Netherlands J. Zool.*, **26**, 319–44.

Krebs, C. R., Gaines, M. S., Keller, B. L., Myers, J. H. & Tamarin, R. H. (1973). Population cycles in small rodents. *Science*, **179**, 35–41.

Kuhme, W. (1963). Erganzende Beobachtungen an afrikanischen Elefanten im Freigehege. *Z. Tierpsychol.*, **20**, 66–79.

Kurt, F. (1974). Remarks on the social structure and ecology of the Ceylon elephant in the Yala National Park. In *The Behaviour of Ungulates and its Relation to Management*, ed. V. Geist & F. Walther, pp. 618–34. IUCN public., new series no. 24, Morges: IUCN.

Kurtén, B. (1968). *Pleistocene Mammals of Europe.* Chicago: Aldine.

Kurtén, B. & Anderson, E. (1980). *Pleistocene Mammals of North America.* New York: Columbia University Press.

Lamprey, H. F. (1983). Pastoralism yesterday and today: the overgrazing problem. In *Ecosystems of the World. 13 Tropical Savannas*, ed. F. Bourliere, pp. 643–66. Amsterdam: Elsevier.

Lamprey, H. F., Bell, R. H. V., Glover, P. E. & Turner, M. J. (1967). Invasion of the Serengeti National Park by elephants. *E. Afr. Wildl. J.*, **5**, 151–66.

Lang, E. M. (1961). Beobachtungen am Indischen Panzernashorn. *Zool. Garten.*, **25**, 369–409.

Lang, E. M. (1967). Einige biologische Daten vom Panzernashorn. *Rev. Suisse Zool.*, **74**, 603–7.

Lang, E. M. (1980). Observations on growth and molar change in the African elephant. *Afr. J. Ecol.*, **18**, 217–34.

Lang, H. (1920), The white rhinoceros of the Belgian Congo (General Account of habits, physical features, distribution, habitat). *Zool. Soc. Bull.*, **23**, 67–92.

Lang, H. (1923). Recent and historical notes on the square-lipped rhinoceros. *J. Mammal.*, **4**, 155–63.

Langer, P. (1976). Functional anatomy of the stomach of hippopotamus. *S. Afr. J. Sci.*, **72**, 12–6.

Langer, P. (1984). Anatomical and nutritional adaptations in wild herbivores. In *Herbivore Nutrition in the Tropics and Subtropics*, ed. F. M. C. Gilchrist & R. I. Mackie, pp. 185–203. Craighall, South Africa: The Science Press.

Langman, V. A. (1973). Radio-tracking giraffe for ecological studies. *J. Sth. Afr. Wildl. Mgmt. Ass.*, **3**, 75–8.

Langman, V. A. (1977). Cow-calf relationships in giraffe. *Z. Tierpsychol.*, **43**, 264–86.

Lark. R. M. (1984). A comparison between techniques for estimating the ages of African elephants. *Afr. J. Ecol.*, **22**, 69–72.

Laurie, W. A. (1978). The ecology and behaviour of the greater one-horned rhinoceros. PhD thesis, Cambridge University.

Laurie, W. A. (1982). Behavioural ecology of the greater one-horned rhinoceros. *J. Zool., Lond.*, **196**, 307–42.

Laws, R. M. (1966). Age criteria for the African elephant. *E. Afr. Wildl. J.*, **4**, 1–37.

Laws, R. M. (1968a). Dentition and aging of the hippopotamus. *E. Afr. Wildl. J.*, **6**, 19–52.

Laws, R. M. (1968b). Interactions between elephant and hippopotamus populations and their environments. *E. Afr. Agric. For. J.*, **33**, 140–47.

Laws, R. M. (1969a). Aspects of reproduction in the African elephant. *J. Reprod. Fert., Suppl.*, **6**, 193–217.

Laws, R. M. (1969b). The Tsavo Research Project. *J. Reprod. Fert., Suppl.*, **6**, 495–531.

Laws, R. M. (1970). Elephants as agents of habitat and landscape change in East Africa. *Oikos*, **21**, 1–15.

Laws, R. M. (1974). Behaviour, dynamics, and management of elephant populations. In

The Behaviour of Ungulates and its Relation to Management, ed. V. Geist & F. Walther, pp. 513–29. IUCN public., new series no. 24, Morges: IUCN.

Laws, R. M. (1981a). Experiences in the study of large mammals. In *Dynamics of Large Mammal Populations*, ed. C. W. Fowler & T. D. Smith, pp. 19–45. New York: Wiley.

Laws, R. M. (1981b). Large mammal feeding strategies and related overabundance problems. In *Management of Locally Abundant Wild Mammals*, ed. P. A. Jewell, S. Holt & D. Hart, pp. 217–232. New York: Academic Press.

Laws, R. M. (1984). Hippopotamuses. In *The Encyclopaedia of Mammals*, ed. D. Macdonald, vol. 2, pp. 506–11. London: George Allen & Unwin.

Laws, R. M. & Clough, G. (1966). Observations on reproduction in the hippopotamus. In *Comparative Biology of Reproduction in Mammals*, ed. I. W. Rowlands, pp. 117–40. Symp. Zool. Soc. London No. 15.

Laws, R. M. & Parker, I. S. C. (1968). Recent studies on elephant populations in East Africa. In *Comparative Nutrition of Wild Animals*, ed. M. A. Crawford, pp. 319–59. Symp. Zool. Soc. London No. 21.

Laws, R. M., Parker, I. S. C. & Johnstone, R. C. B. (1970). Elephants and habitats in North Bunyoro, Uganda. *E. Afr. Wildl. J.*, **8**, 163–80.

Laws, R. M., Parker, I. S. C. & Johnstone, R. C. B. (1975) *Elephants and their Habitats. The Ecology of Elephants in North Bunyoro, Uganda.* Oxford: Clarendon Press.

Leader-Williams, N. (1980). Population dynamics and regulation of reindeer introduced into South Georgia. *J. Wildl. Manage.*, **44**, 640–57.

Ledger, H. P. (1963). Weights of some East African mammals. *E. Afr. Wildl. J.*, **1**, 123–4.

Ledger, H. M. (1964). Weights of some East African mammals:2. *E. Afr. Wildl. J.*, **2**, 159.

Ledger, H. P. (1968). Body composition as a basis for a comparative study of some East African mammals. In *Comparative Nutrition of Wild Animals*, ed. M. A. Crawford, pp. 289–310. Symp. Zool. Soc. London No. 21.

Lee, P. C. (1987). Allomothering among African elephants. *Anim. Behav.*, **35**, 278–91.

Lee, P. C. & Moss, C. J. (1986). Early maternal investment in male and female elephant calves. *Behav. Ecol. Sociobiol.*, **18**, 353–61.

Lent, P. C. (1974). Mother-infant relationships in ungulates. In *The Behaviour of Ungulates and its Relation to Management*, ed. V. Geist & F. Walther, pp. 14–55. IUCN public., new series no. 24, Morges: IUCN.

Leopold, A. S. (1968). Ecological objectives in park management. *E. Afr. Agric. For. J.*, **33**, 168–72.

Leopold, A. S., Cain, S. A., Cottam, C. M., Gabrielson, I. N. & Kimball, T. L. (1963). Wildlife management in the national parks. *Trans. N. Amer. Wildl. & Nat. Res. Conf.*, **28**, 28–45.

Leuthold, B. M. (1979). Social organization and behaviour of giraffe in Tsavo East National Park. *Afr. J. Ecol.*, **17**, 19–34.

Leuthold, B. M. & Leuthold, W. (1972). Food habits of giraffe in Tsavo National Park, Kenya. *E. Afr. Wildl. J.*, **10**, 129–41.

Leuthold, B. M. & Leuthold, W. (1978). Ecology of giraffe in Tsavo East National Park, Kenya. *E. Afr. Wildl. J.*, **16**, 1–20.

Leuthold, W. (1966). Variations in territorial behaviour of Uganda kob. *Behaviour*, **27**, 215–58.

Leuthold, W. (1970). Observations on the social organisation of impala. *Z. Tierpsychol.*, **27**, 693–721.

Leuthold, W. (1971). Freilandsbeobachtungen an Giraffengazellen in Tsavo National Park, Kenya. *Z. Saugetierk.*, **36**, 19–37.

Leuthold, W. (1972). Home range, movements and food of a buffalo herd in Tsavo National Park. *E. Afr. Wildl. J.* **10**, 237–243.

Leuthold, W. (1974). Observations on home range and social organisation of lesser kudu. In *The Behaviour of Ungulates and its Relation to Management*, ed. V. Geist & F. Walther, pp. 206–34. IUCN public., new series no. 24, Morges: IUCN.

Leuthold, W. (1976a). Age structure of elephants in Tsavo National Park, Kenya. *J. Appl. Ecol.*, **13**, 435–44.

Leuthold, W. (1976b). Group size in elephants of Tsavo National Park and possible factors influencing it. *J. Anim. Ecol.*, **45**, 425–39.

Leuthold, W. (1977a). *African Ungulates. A Comparative Review of their Ethology and Behavioural Ecology*. Zoophysiology and Ecology No. 8, New York: Springer Verlag. 307pp.

Leuthold, W. (1977b). A note on group size and composition in the oribi. *Z. Saugetierk.*, **42**, 233–5.

Leuthold, W. (1977c). Spatial organization and strategy of habitat utilization of elephants in Tsavo National Park, Kenya. *Z. Saugetierk.*, **42**, 358–79.

Leuthold, W. (1977d). Changes in tree populations of Tsavo East National Park, Kenya. *E. Afr. Wildl. J.*, **15**, 61–9.

Leuthold, W. (1979). The lesser kudu *Tragelephus imberbis* (Blyth, 1869). Ecology and behaviour of an African antelope. *Saugetierk. Mitt.*, **27**, 1–75.

Leuthold, W. & Leuthold, B. M. (1975). Patterns of social grouping in ungulates of Tsavo National Park, Kenya. *J. Zool. Lond.*, **175**, 405–20.

Leuthold, W. & Leuthold, B. M. (1976). Density and biomass of ungulates in Tsavo East National Park, Kenya. *E. Afr. Wildl. J*, **14**, 49–58.

Leuthold, W. & Sale, J. B. (1973). Movements and patterns of habitat utilization of elephants in Tsavo National Park, Kenya. *E. Afr. Wildl. J.*, **11**, 369–84.

Lewis, D. M. (1984). Demographic changes in Luangwa Valley elephants. *Biol. Cons.*, **29**, 7–14.

Lewis, D. M. (1986). Disturbance effects on elephant feeding: evidence for compression in Luangwa Valley, Zambia. *Afr. J. Ecol.*, **24**, 227–41.

Lidicker, W. Z. (1975). The role of dispersal in the population ecology of small mammals. In *Small Mammals: Their Productivity and Population Dynamics*, ed. F. B. Golley, K. Petrusewicz & L. Ryszkowski, pp. 103–28. Cambridge: Cambridge University Press.

Lightfoot, C. J. (1978). The feeding ecology of giraffe in the Rhodesian middleveld as a basis for the determination of carrying capacity. MSc thesis, University of Rhodesia.

Lindemann, H. (1982). African rhinoceroses in captivity. Thesis, University of Copenhagen.

Lindstedt, S. L. & Boyce, M. S. (1985). Seasonality, fasting endurance, and body size in mammals. *Am. Nat.*, **125**, 873–8.

Lindstedt, S. L. & Calder, W. A. III. (1981). Body size, physiological time and longevity of homeothermic animals. *Q. Rev. Biol.*, **56**, 1–16.

Liu, T.-S. & Li, X.-G. (1984). Mammoths in China. In *Quarternary Extinctions*, ed. P. S. Martin & R. G. Klein, pp. 517–27. New York: Academic Press.

Livingstone, D. A. (1975). Late quarternary climatic change in Africa. *Ann. Rev. Ecol. Syst.*, **6**, 249–80.

Lock, J. M. (1972). The effect of hippopotamus grazing in grasslands. *J. Ecol.*, **60**, 445–67.

Lock, J. M. (1985). Recent changes in the vegetation of Queen Elizabeth National Park, Uganda. *Afr. J. Ecol.*, **23**, 63–5.

Lomnicki, A. (1978). Individual differences between animals and the natural regulation of their numbers. *J. Anim. Ecol.*, **47**, 461–75.

Lomnicki, A. (1982). Individual heterogeneity and population regulation. In *Current Problems in Sociobiology*, ed. King's College Sociobiology Group, Cambridge, pp. 153–67. Cambridge: Cambridge University Press.

Lomolino, M. V. (1985). Body size of mammals on islands: the island rule reexamined. *Am. Nat.*, **125**, 310–6.

Lorius, C., Jouzel, J., Ritz, C., Merlivat, L., Barkov, N. I., Korotkevich, Y. S. & Kotlyakov, V. M. (1985). A 150,000 year climatic record from Antarctic ice. *Nature*, **316**, 591–6.

Lott, D. F. (1974). Sexual and aggressive behaviour of American bison. In *The Behaviour of Ungulates and its Relation to Management*. ed. V. Geist & F. Walther, pp. 382–94. IUCN public., new series no. 24, Morges: IUCN.

Lott, D. F. (1979). Dominance relations and breeding rate in mature male American bison. *Z. Tierpsychol.*, **49**, 418–32.

Loutit, B. D., Louw, G. N. & Seely, M. K. (1987). Preliminary observations of food preferences and chemical composition of the diet of the desert-dwelling black rhinoceros. *Madoqua*, **15**, 35–54.

Low, W. A., Tweedie, R. L., Edwards, C. B. H., Hodder, R. M., Malafant, K. W. J. & Cunningham, R. B., (1981). The influence of environment on daily maintenance behaviour of free-ranging shorthorn cows in central Australia. II Multivariate analysis of duration and incidence of activities. *Appl. Anim. Ethol.*, **7**, 27–38.

MacArthur, R. H. & E. O. Wilson, (1967). *The Theory of Island Biogeography.* Princeton, New Jersey: Princeton University Press. 203pp.

Macdonald, D. (ed.) (1984). *The Encyclopaedia of Mammals*. vol. 2. London: George Allen & Unwin. 895pp.

Mace, G. M. & Harvey, P. H. (1983). Energy constraints on home range size. *Am. Nat.*, **121**, 120–32.

Mackie, C. S. (1973). Interactions between the hippopotamus and its environment on the Lundi River. Certificate in Field Ecology thesis, University of Rhodesia.

Mackie, C. S. (1976). Feeding habits of the hippopotamus on the Lundi River, Rhodesia. *Arnoldia* (*Rhodesia*), **7**, 34, 1–6.

Maglio, V. J. (1973). Origin and evolution of the Elephantidae. *Trans. Am. Phil Soc.*, **n.s. 63**, 3, 1–149.

Maglio, V. J. (1978). Patterns of faunal evolution. In *Evolution of African Mammals*, ed. V. J. Maglio & H. B. S. Cooke, pp. 603–19. Cambridge, Mass: Harvard University Press.

Maglio, V. J. & Cooke, H. B. S. (eds.). (1978). *Evolution of African Mammals*. Cambridge, Mass: Harvard University Press.

Malpas, R. C. (1977). The condition and growth of elephants in Uganda. *J. Appl. Ecol.*, **14**, 489–504.

Malpas, R. C. (1978). The ecology of the African elephant in Uganda. PhD thesis, University of Cambridge.

Marcus, L. F. & Berger, R. (1984). The significance of radiocarbon dates for Rancho La Brea. In *Quaternary Extinctions*, ed. P. S. Martin & R. G. Klein, pp. 159–83. Tucson: University of Arizona Press.

Markgraf, V. (1985). Late Pleistocene faunal extinctions in southern Patagonia. *Science*, **228**, 1110–2.

Marshall, P. J. & Sayer, J. A. (1976). Population ecology and response to cropping of a hippopotamus population in eastern Zambia. *J. Appl. Ecol.*, **13**, 391–404.

Martin, E. B. & Martin, C. (1982). *Run Rhino Run*. London: Chatto & Windus.

Martin, P. S. (1967). Prehistoric overkill. In *Pleistocene Extinctions: The Search for a Cause*, ed. P. S. Martin & H. E. Wright, pp. 75–120. New Haven, Conn.: Yale University Press.

Martin, P. S. (1973). The discovery of America. *Science*, **179**, 969–74.

Martin, P. S. (1982). The pattern and meaning of holarctic mammoth extinction. In *The Paleoecology of Beringia*, ed. D. M. Hopkins, J. V. Matthews, C. S. Schweger & S. B. Young, pp. 398–408. New York: Academic Press.

Martin, P. S. (1984a). Prehistoric overkill: the global model: In *Quaternary Extinctions*, ed. P. S. Martin & R. G. Klein, pp. 354–403. Tucson: University of Arizona Press.

Martin, P. S. (1984b). Catastrophic extinctions and late Pleistocene blitzkrieg: two radiocarbon tests. In *Extinctions*, ed. M. Nitecki, pp. 153–89. Chicago: University of Chicago Press.

Martin, P. S. & Guilday, J. E. (1967). A bestiary for Pleistocene biologists. In *Pleistocene Extinctions: The Search for a Cause*, ed. P. S. Martin & H. E. Wright, pp. 1–62. New Haven, Conn.: Yale University Press.

Martin, P. S. & Klein, R. G. (1984). *Quaternary Extinctions: a Prehistoric Revolution*. Tucson: University of Arizona Press. 892pp.

Martin, P. S. & Wright, H. E. (eds.). (1967). *Pleistocene Extinctions: The Search for a Cause*. New Haven, Conn.: Yale University Press, 453pp.

Martin, R. B. (1978). Aspects of elephant social organisation. *Rhodesia Science News*, **12**, 184–7.

Martin, R. B. & Taylor, R. D. (1983). Wildlife conservation in a regional land-use context: the Sebungwe region of Zimbabwe. In *Management of Large Mammals in African Conservation Areas*, ed. R. N. Owen-Smith, pp. 249–70. Pretoria: Haum.

Martin, R. D. & MacLarnon, A. M. (1985). Gestation period, neonatal size and maternal investment in placental mammals. *Nature*, **313**, 220–3.

Mason, D. R. (1982). Studies on the biology and ecology of the warthog in Zululand. DSc thesis, University of Pretoria.

Mason, D. R. (1985a). Postnatal growth and physical condition of warthogs in Zululand. *S. Afr. J. Wildl. Res.*, **15**, 89–97.

Mason, D. R. (1985b). *Monitoring of Ungulate Population Structure in the Kruger National Park – Report on Survey during August, September and October 1984*. Skukuza: Kruger National Park Dept. of Research and Information Memorandum.

Mason, D. R. & van der Walt, P. F. (1984). Sex and age data from cropping of buffalo in the Kruger National Park. *Koedoe*, **27**, 73–8.

Matthews, J. V. (1982). East Beringia during late Wisconsin time: a review of the biotic evidence. In *Paleoecology of Beringia*, ed. D. M. Hopkins, J. V. Matthews, C. E. Schweger & S. B. Young, pp. 127–50. New York: Academic Press.

Maynard Smith, J. (1980). A new theory of sexual investment. *Behav. Ecol. Sociobiol.*, **7**, 247–51.

McCullagh, K. (1969). The growth and nutrition of the African elephant. II The chemical nature of the diet. *E. Afr. Wildl. J.*, **7**, 91–7.

McCullough, D. R. (1969). The Tule elk. Its history, behavior and ecology. *Univ. Calif. Public. Zool.*, **88**, 1-191.

McKay, G. M. (1973). *Behavior and ecology of the Asiatic elephant in southeastern Ceylon.* Smithsonian Contrib. Zool. no. 125, 113 pp.

McNab, B. K. (1963). Bioenergetics and the determination of home range size. *Am. Nat.*, **97**, 133–40.

McNaughton, S. J. (1976). Serengeti migratory wildebeest: facilitation of energy flow by grazing. *Science*, **191**, 92–3.

McNaughton, S. J. (1979). Grazing as an optimization process: grass-ungulate relationships in the Serengeti. *Am. Nat.*, **113**, 691–703.

McNaughton, S. J. (1984). Grazing lawns: animals in herds, plant form and coevolution. *Am. Nat.*, **124**, 863–86.

McNaughton, S. J. (1985). Ecology of a grazing ecosystem: the Serengeti. *Ecol. Monogr.*, **55**, 259–94.

Mead, J. J. & Meltzer, D. J. (1984). North American late Quarternary extinctions and the radiocarbon record. In *Quaternary Extinctions*, ed. P. S. Martin & R. G. Klein, pp. 440–50. Tucson: University of Arizona Press.

Meinertzhagen, R. (1938). Some weights and measurements of large mammals. *Proc. Zool. Soc. London.*, **A108**, 433–9.

Melton, D. A. (1978). Undercounting bias of helicopter censuses in the Umfolozi Game Reserve. *Lammergeyer* (*Natal*), **26**, 1–6.

Melton, D. A. (1985). The status of elephants in northern Botswana. *Biol. Cons.*, **31**, 317–33.

Mentis, M. T. (1972). A review of some life history features of the large herbivores of Africa. *Lammergeyer* (*Natal*), **16**, 1–89.

Merz, G. (1981). Recherches sur la biologie de nutrition et les habitats preferes de l'elephant de foret. *Mammalia*, **45**, 299–312.

Merz, G. (1986a). Counting elephants in tropical rain forests with particular reference to Tai National Park, Ivory Coast. *Afr. J. Ecol.*, **24**, 61–8.

Merz, G. (1986b). Movement patterns and group size of the African forest elephant in the Tai National Park, Ivory Coast. *Afr. J. Ecol.*, **24**, 133–6.

Millar, J. S. (1977). Adaptive features of mammalian reproduction. *Evol.*, **31**, 370–86.

Millar, J. S. & Zammuto, R. M. (1983). Life histories of mammals: an analysis of life tables. *Ecology*, **64**, 631–5.

Miller, K. R. (1983). Matching conservation goals to diverse conservation areas: a global perspective. In *Management of Large Mammals in African Conservation Areas*, ed. R. N. Owen-Smith, pp. 1–12. Pretoria: Haum.

Milton, K. & May, M. (1976). Body weight, diet and home range area in primates. *Nature*, **259**, 459–62.

Mitchell, B., Staines, B. W. & Welch, D. (1977). *Ecology of Red Deer*. Banchory: Institute of Terrestrial Ecology.

Moen, A. N. (1973). *Wildlife Ecology*. San Francisco: Freeman. 458 pp.

Morris, N. E. & Hanks, J. (1974). Reproduction in the bushbuck. *Arnoldia* (*Rhodesia*), **7**, 1, 1–8.

Moss, C. J. (1983). Oestrous behaviour and female choice in the African elephant. *Behaviour*, **86**, 167–96.

Mossman, A. S. & Mossman, H. W. (1962). Ovulation, implantation and fetal sex ratio in impala. *Science*, **137**, 869.

Mueller-Dombois, D. (1972). Crown distortion and elephant distribution in the woody vegetation of Ruhunu National Park, Ceylon. *Ecology*, **53**, 208–26.

Mukinya, J. G. (1973). Density, distribution, population structure and social organization of the black rhinoceros in Masai Mara Game Reserve. *E. Afr. Wildl. J.*, **11**, 385–400.

Mukinya, J. G. (1977). Feeding and drinking habits of the black rhinoceros in Masai Mara Game Reserve. *E. Afr. Wildl. J.*, **15**, 125–38.

Müller-Beck, H. (1982). Late Pleistocene man in northern Alaska and the mammoth-steppe biome. In *Paleoecology of Beringia*, ed. D. M. Hopkins, J. V. Matthews, C. E. Schweger & S. B. Young, pp. 329–52. New York: Academic Press.

Murray, M. G. (1980). Social structure of an impala population. D. Phil. thesis, University of Rhodesia.

Murray, M. G. (1982a). The rut of impala: aspects of seasonal mating under tropical conditions. *Z. Tierpsychol.*, **59**, 319–37.

Murray, M. G. (1982b). Home range, dispersal and clan system of impala. *Afr. J. Ecol.*, **20**, 253–269.

Murray, P. (1984). Extinctions downunder: a bestiary of extinct Australian late Pleistocene monotremes and marsupials. In *Quarternary Extinctions*, ed. P. S. Martin & R. G. Klein, pp. 600–28. Tucson: University of Arizona Press.

Mwalyosi, R. B. B. (1977). A count of large mammals in Lake Manyara National Park. *E. Afr. Wildl. J.*, **15**, 333–5.

Mwalyosi, R. B. B. (1987). Decline of *Acacia tortilis* in Lake Manyara National Park, Tanzania. *Afr. J. Ecol.*, **25**, 51–4.

Myers, N. (1972). National Parks in savanna Africa. *Science*, **178**, 1255–63.

Myers, N. (1973). Tsavo National Park, Kenya, and its elephants: an interim appraisal. *Biol. Cons.*, **5**, 123–32.

Nagy, K. A. (1987). Field metabolic rate and food requirement scaling in mammals and birds. *Ecol. Monogr.*, **57**, 111–28.

Napier Bax, P. & Sheldrick, D. L. W. (1963). Some preliminary observations on the food of elephant in the Tsavo Royal National Park (East) of Kenya. *E. Afr. Wildl. J.*, **1**, 40–53.

Naylor, J. N., Caughley, G. J., Abel, N. O. & Liberg, O. N. (1973). *Luangwa Valley Conservation and Development Project, Zambia. Game Management and Habitat manipulation.* Rome: FAO Report.

Nge'the, J. C. (1976). Preference and daily intake of five East African grasses by zebras. *J. Range Manage*, **29**, 5–10.

Nge'the, J. C. & Box, T. W. (1976). Botanical composition of eland and goat diets in an *Acacia* grassland community in Kenya. *J. Range Manage.*, **29**, 290–93.

Norton, P. M. (1981). Activity patterns of the klipspringer in two areas of the Cape Province. *S. Afr. J. Wildl. Res.*, **11**, 126–34.

Norton-Griffiths, M. (1975). The numbers and distribution of large mammals in Ruaha National Park, Tanzania, *E. Afr. Wildl. J.*, **13**, 121–40.

Novellie, P. A., Manson, J. & Bigalke R. C. (1984). Behavioural ecology and communiction in the Cape grysbok. *S. Afr. J. Zool.*, **19**, 22–30.

O'Connor, T. G. & Campbell, B. M. (1986). Hippopotamus habitat relationships on the Lundi River, Gonarezhou National Park, Zimbabwe. *Afr. J. Ecol*, **24**, 7–26.

Oftedal, O. T. (1984). Milk composition, milk yield and energy output at peak lactation. In *Lactation Strategies*, Symp. Brit. Ecol. Soc., No. 51, pp. 33–85.

Oliver, M. D. N., Short, N. R. M. & Hanks, J. (1978). Population ecology of oribi, grey rhebuck and mountain reedbuck in Highmoor State Forest Land, Natal. *S. Afr. J. Wildl. Res.*, **8**, 95–105.

Olivier, R. C. D. (1978). On the ecology of the Asian elephant with particular reference to Malaya and Sri Lanka. PhD thesis, University of Cambridge.

Olivier, R. C. D. (1982). Ecology and behavior of living elephants: bases for assumptions concerning the extinct woolly mammoths. In *Paleoecology of Beringia*, ed. D. M. Hopkins, J. V. Matthews, C. E. Schweger & S. B. Young, pp. 291–306. New York: Academic Press.

Olivier, R. C. D. & Laurie, W. A. (1974). Habitat utilisation by hippopotamus in the Mara River. *E. Afr. Wildl. J.*, **12**, 249–72.

Ottochilo, W. K. (1986). Population estimates and distribution patterns of elephants in the Tsavo ecosystem, Kenya, in 1980. *Afr. J. Ecol.*, **24**, 53–7.

Owaga, M. L. (1975). The feeding ecology of wildebeest and zebra in the Athi-Kaputei plains. *E. Afr. Wildl. J.*, **13**, 375–83.

Owen-Smith, G. (1986). The Kaokoveld, South West Africa/Namibia's threatened wilderness. *Afr. Wildl.*, **40**, 104–13.

Owen-Smith, N. (1971a). Territoriality in the white rhinoceros. *Nature*, **231**, 294–6.

Owen-Smith, N. (1971b). The contribution of radio telemetry to a study of the white rhinoceros. *Symposium on Biotelemetry, Pretoria, 1971.* Pretoria: Council for Scientific and Industrial Research.

Owen-Smtih, N. (1972). Territoriality: the example of the white rhinoceros. *Zoologica Africana*, **7**, 273–80.

Owen-Smtih, N. (1973). The behavioural ecology of the white rhinoceros. PhD thesis, University of Wisconsin.

Owen-Smith, N. (1974a). The social system of the white rhinoceros. In *The Behaviour of Ungulates and its Relation to Management*, ed. V. Geist & F. Walther, pp. 341–51. IUCN public., new series no. 24, Morges: IUCN.

Owen-Smith, N. (1974b). Minisender decken Verhalten von Nashornen auf.. *Umschau*, **74**, 119–20.

Owen-Smith, N. (1975). The social ethology of the white rhinoceros. *Z. Tierpsychol.*, **38**, 337–84.

Owen-Smith, N. (1977). On territoriality in ungulates and an evolutionary model. *Q. Rev. Biol.*, **52**, 1–38.

Owen-Smith, N. (1979). Assessing the foraging efficiency of a large herbivore, the kudu. *S. Afr. J. Wildl. Res.*, **9**, 102–10.

Owen-Smith, N. (1981). The white rhino overpopulation problem, and a proposed solution. In *Problems in Management of Locally Abundant Wild Mammals*, ed. P. A. Jewell, S. Holt & D. Hart, pp. 129–50. New York: Academic Press.

Owen-Smith, N. (1982). Factors influencing the consumption of plant products by large herbivores. In *The Ecology of Tropical Savannas*, ed. B. J. Huntley & B. H. Walker, pp. 359–404. Berlin: Springer-Verlag.

Owen-Smith, N. (1983). Dispersal and the dynamics of large herbivore populations in enclosed areas. In *Management of Large Mammals in African Conservation Areas*, ed. R. N. Owen-Smith, pp. 127–43. Pretoria: Haum.

Owen-Smith, N. (1984). Spatial and temporal components of the mating systems of kudu bulls and red deer stags. *Anim. Behav.*, **32**, 321–32.

Owen-Smith, N. (1985). Niche separation among African ungulates. In *Species and Speciation*, ed. E. S. Vrba, pp. 167–71. Transvaal Mus. Monogr. No. 4, Pretoria: Transvaal Museum.

Owen-Smith, N. (1988 in press). Morphological factors and their consequences for resource partitioning among African savanna ungulates: a simulation modelling approach. In *Patterns in the Structure of Mammalian Communities*. ed. D. W. Morris, Z. Abramsky, B. J. Fox & M. L. Willig, Lubbock, Texas: Texas Tech Museum Special Publication Series.

Owen-Smith, N. & Novellie, P. (1982). What should a clever ungulate eat? *Am. Nat.*, **119**, 151–78.

Packer, C. (1983). Sexual dimorphism: the horns of African antelopes. *Science*, **221**, 1191–3.

Paraa, R. (1978). Comparison of foregut and hindgut fermentation in herbivores. In *The Ecology of Arboreal Folivores*, ed. G. G. Montgomery, pp. 205–29. Washington, D.C.: Smithsonian Institution Press.

Parker, G. A. (1974). Assessment strategy and the evolution of animal conflicts. *J. Theor. Biol.*, **47**, 223–43.

Parker, I. S. C. (1983). The Tsavo story: an ecological case history. In *Management of Large Mammals in African Conservation Areas*, ed. R. N. Owen-Smith, pp. 37–50. Pretoria: Haum.

Parker, I. S. C. & Amin, M. (1983). *Ivory Crisis*. London: Chatto & Windus.

Patterson, H. E. H. (1985). The Recognition Concept of species. In *Species and Speciation*, ed. E. S. Vrba, pp. 21–30. Transvaal Mus. Monogr. No. 4, Pretoria: Transvaal Museum.

Payne, K. B., Langbauer, W. R. Jr. & Thomas, E. M. (1986). Infrasonic calls of the Asian elephant. *Behav. Ecol. Sociobiol.*, **18**, 297–302.

Pellew, R. A. (1981). The giraffe and its *Acacia* food resource in the Serengeti National Park. PhD thesis, University of Cambridge.

Pellew, R. A. (1983a). The giraffe and its food resource in the Serengeti. II. Response of the population to changes in the food supply. *Afr. J. Ecol.*, **21**, 269–83.

Pellew, R. A. (1983b). Modelling and the systems approach to management problems: the *Acacia*/elephant problem in the Serengeti. In *Management of Large Mammals in African Conservation Areas*, ed. R. N. Owen-Smith, pp. 93–114. Pretoria: Haum.

Pellew, R. A. (1983c). The impacts of elephant, giraffe and fire upon *Acacia tortilis* woodlands of the Serengeti. *Afr. J. Ecol.*, **21**, 41–74.

Pellew, R. A. (1984a). Giraffe and okapi. In *The Encyclopaedia of Mammals*, vol. 2, ed. D. Macdonald, pp. 534–41. London: George Allen & Unwin.

Pellew, R. A. (1984b). The feeding ecology of a selective browser, the giraffe. *J. Zool. Lond.*, **202**, 57–81.

Pellew, R. A. (1984c). Food consumption and energy budgets of the giraffe. *J. Appl. Ecol.*, **21**, 141–59.

Pennycuick, L. (1975). Movements of the migratory wildebeest population in the Serengeti. *E. Afr. Wildl. J.*, **13**, 65–87.

Penzhorn, B. L. (1974). Sex and age composition and dimensions of the springbok population in the Mountain Zebra National Park. *J. Sth. Afr. Wildl. Mgmt. Ass.*, **4**, 63–6.

Penzhorn, B. L. (1975). Behaviour and population ecology of the Cape mountain zebra in the Mountain Zebra National Park. DSc thesis, University of Pretoria.

Penzhorn, B. L., Robbertse, P. J. & Olivier, M. C. (1974). The influence of the African elephant on the vegetation of the Addo Elephant National Park. *Koedoe*, **17**, 137–58.

Perry, J. S. (1953). The reproduction of the African elephant. *Philos. Trans. Roy. Soc. Lond.*, **B237**, 93–149.

Peters, R. H. (1983). *The Ecological Implications of Body Size.* Cambridge: Cambridge University Press. 329pp.

Peters, R. H. & Raelson, J. V. (1984). Relations between individual size and mammalian population density. *Am. Nat.*, **124**, 498–517.

Peters, R. H. & Wassenberg, K. (1983). The effect of body size on animal abundance. *Oecologia*, **60**, 89–96.

Petrides, G. A. (1974). The overgrazing cycle as a characterisitc of tropical savanna and grasslands in Africa. *Proc. 1st Int. Congr. Ecol.*, pp. 86–91. Wageningen.

Petrides, G. A. & Swank, W. G. (1965). Population densities and range-carrying capacity for large mammals in Queen Elizabeth National Park, Uganda. *Zoologica Africana*, **1**, 209–25.

Phillips, A. M. III. (1984). Shasta ground sloth extinction: fossil packrat midden evidence from the western Grand Canyon. In *Quarternary Extinctions*, ed. P. S. Martin & R. G. Klein, pp. 148–58. Tucson: University of Arizona Press.

Phillipson, J. (1975). Rainfall, primary production and carrying capacity of Tsavo National Park (East), Kenya. *E. Afr. Wildl. J.*, **13**, 171–201.

Pianka, E. R. (1970). On r- and K-selection. *Am. Nat.*, **104**, 592–7.

Pianka, E. R. (1974). *Evolutionary Ecology.* New York: Harper & Row. 356pp.

Pickett, S. T. A. & White, P. S. (eds.) (1985). *The Ecology of Natural Disturbance and Patch Dynamics.* New York: Academic Press. 496pp.

Pienaar, U. de V. (1963). The large mammals of the Kruger National Park – their distribution and present-day status. *Koedoe*, **6**, 1–37.

Pienaar, U. de V. (1969). Observations on development biology, growth and some aspects of the population ecology of African buffalo in the Kruger National Park. *Koedoe*, **12**, 29–52.

Pienaar, U. de V. (1970). The recolonisation history of the square-lipped (white) rhinoceros in the Kruger National Park (October 1961-November 1969). *Koedoe*, **13**, 157–69.

Pienaar, U. de V. (1982). The Kruger Park saga (1898–1981). Mimeographed paper presented at the workshop on Management of Large Mammals in African

Conservation Areas, Kruger National Park, September 1982, 38pp.

Pienaar, U. de V. (1983). Management by intervention: the pragmatic/economic option. In *Management of Large Mammals in African Conservation Areas*, ed. R. N. Owen-Smith, pp. 23–36. Pretoria: Haum.

Pienaar, U. de V., van Wyk, P. & Fairall, N. (1966a). An experimental cropping scheme of hippopotami in the Letaba River of the Kruger National Park. *Koedoe*, **9**, 1–33.

Pienaar, U. de V., van Wyk, P. & Fairall, N. (1966b). An aerial census of elephant and buffalo in the Kruger National Park, and the implications thereof on intended management schemes. *Koedoe*, **9**, 40–107.

Pilgram, T. & Western, D. (1986). Managing African elephant for ivory production through ivory trade restrictions. *J. Appl. Biol.*, **23**, 515–29.

Player, I. C. & Feely, J. M. (1960). A preliminary report on the square-lipped rhinoceros. *Lammergeyer (Natal)*, **1**, 3–23.

Poole, J. H. & Moss, C. J. (1981). Musth in the African elephant. *Nature*, **292**, 830–1.

Pratt, D. M. & Anderson, V. H. (1979). Giraffe cow-calf relationships and social development of the calf in the Serengeti. *Z. Tierpsychol.*, **51**, 233–51.

Ralls, K. (1977). Sexual dimorphism in mammals: avian models and unanswered questions. *Am. Nat.*, **111**, 917–38.

Rawlins, C. G. C. (1979). The breeding of white rhinos in captivity – a comparative survey. *Zool. Gart., NF*, **49**, 1–7.

Reed, C. A. (1970). The extinctions of mammalian megafauna in the Old World late Quarternary. *BioScience*, **20**, 284–8.

Reiss, M. J. (1985). The allometry of reproduction: why larger species invest relatively less in their offspring. *J. Theor. Biol.*, **113**, 529–44.

Reiss, M. J. (1986). Sexual dimorphism in body size – are larger species more dimorphic? *J. Theor. Biol.*, **121**, 163–72.

Remmert, H. (1982). The evolution of man and the extinction of animals. *Naturwissenschaften*, **69**, 524–7.

Reuterwall, C. (1981). Temporal and spatial variability of the calf sex ratio in Scandinavian moose. *Oikos*, **37**, 39–45.

Reynolds, R. J. (1960). White rhinos in captivity. *Int. Zoo Ybk.*, **2**, 42–43.

Rhoades, D. F. (1985). Offensive-defensive interactions between herbivores and plants: their relevance in herbivore population dynamics and ecological theory. *Am. Nat.*, **125**, 205–38.

Riney, T. (1964). The impact of introductions of large herbivores on the tropical environment. IUCN public., new series no. 4, pp. 261–273.

Ripley, S. D. (1952). Territorial and sexual behaviour in the Great Indian rhinoceros: a speculation. *Ecology*, **33**, 570–3.

Ritchie, A. T. A. (1963). The black rhinoceros. *E. Afr. Wildl. J.*, **1**, 54–62.

Ritchie, J. C. & Cwynar, L. C. (1982). The late Quarternary vegetation of the north Yukon. In *Paleoecology of Beringia*, ed. D. M. Hopkins, J. V. Matthews Jr., C. E. Schweger & S. B. Young, pp. 113–26. New York: Academic Press.

Robbins, C. T. & Robbins, B. L. (1979). Fetal and neonatal growth patterns and maternal reproductive effort in ungulates and subungulates. *Am. Nat.*, **114**, 101–16.

Robinette, W. L. & Archer, A. L. (1971). Notes on ageing criteria and reproduction of Thomson's gazelle. *E. Afr. Wildl. J.*, **9**, 83–98.

Robinette, W. L. & Child, G. F. T. (1964). Notes on biology of the lechwe. *Puku*, **2**, 84–117.

Robinette, W. L., Jones, D. A., Geshwiler, J. S. & Low, J. B. (1957). Differential mortality by sex and age among mule deer. *J. Wildl. Manage.*, **21**, 1–16.

Robinson, T. J. (1979). Influence of a nutritional factor on the size differences of the three springbok subspecies. *S. Afr. J. Wildl. Res.*, **14**, 13–15.

Rodgers, D. A. & Elder, W. H. (1977). Movements of elephants in Luangwa Valley, Zambia, *J. Wildl. Manage.*, **41**, 56–62.

Rodgers, W. A. (1977). Seasonal changes in group size amongst five wild herbivore species. *E. Afr. Wildl. J.*, **15**, 175–90.

Roff, D. A. (1974). The analysis of a population model demonstrating the importance of dispersal in a heterogeneous environment. *Oecologia*, **15**, 259–75.

Roff, D. A. (1975). Population stability and the evolution of dispersal in a heterogeneous environment. *Oecologia*, **19**, 217–37.

Rosenzweig, M. L. (1968). Net primary production of terrestrial communities: prediction from climatological data. *Am. Nat.*, **102**, 74–6.

Roth, H. H., Kerr, M. A. & Posselt, J. (1972). Studies on the utilization of semi-domesticated eland in Rhodesia. V Reproduction and herd increase. *Z. Tierzuchtung und Zuchtungsbiologie*, **89**, 69–83.

Rubenstein, D. I. (1980). On the evolution of alternative mating strategies. In *Limits to Action*, ed. J. E. Staddon, pp. 65–100. New York: Academic Press.

Rutherford, M. C. (1980). Annual plant production-precipitation relations in arid and semi-arid regions. *S. Afr. J. Sci.*, **76**, 53–6.

Sachs, R. (1967). Liveweights and body measurements of Serengeti game animals. *E. Afr. Wildl. J.*, **5**, 24–36.

Sadleir, R. M. F. S. (1969). *The Ecology of Reproduction in Wild and Domestic Animals.* London: Methuen. 321pp.

Santiapillai, C., Chambers, M. R. & Ishwaran, N. (1984). Aspects of the ecology of the Asian elephant in the Ruhunu National Park, Sri Lanka. *Biol. Cons.*, **29**, 47–61.

Sauer, J. J. C., Theron, G. K. & Skinner, J. D. (1977). Food preferences of giraffe in the arid bushveld of the western Transvaal. *S. Afr. J. Wildl. Res.*, **7**, 53–9.

Sayer, J. A. & Rahka, A. M. (1974). The age of puberty in the hippopotamus in the Luangwa River in eastern Zambia. *E. Afr. Wildl. J.*, **12**, 227–37.

Sayer, J. A. & van Lavieren, L. P. (1975). The ecology of the Kafue lechwe population of Zambia before the operation of hydroelectric dams on the Kafue River. *E. Afr. Wildl. J.*, **13**, 9–37.

Schaller, G. B. (1967). *The Deer and the Tiger. A Study of Wildlife in India.* Chicago: University of Chicago Press. 370pp.

Schaller, G. B. (1972). *The Serengeti Lion. A Study of Predator-Prey Relationships.* Chicago: University of Chicago Press. 480pp.

Schaurte, W. T. (1969). Uber das geburt eines Breitmaulnashornes in Wildschutzgebiet Krugersdorp in Transvaal. *Saugetierk. Mitt.*, **17**, 158–60.

Schenkel, R. (1966). Zum Problem der Territorialitat und des Markierens bei Saugern – am Beispiel des Schwartzen Nashorns und des Lowens. *Z. Tierpsychol.*, **23**, 593–626.

Schenkel, R. & Schenkel-Hulliger, L. (1969a). *Ecology and Behaviour of the Black Rhinoceros. A Field Study.* Mammalia Depicta, Berlin-Hamburg: Paul Parey. 101pp.

Schenkel, R. & Schenkel-Hulliger, L. (1969b). The Javan rhinoceros in Udjong Kulon Nature Reserve, its ecology and behaviour. *Acta Tropica*, **26**, 98–135.

Schmidt-Nielsen, K. (1984). *Scaling. Why is Animal Size So Important?* Cambridge: Cambridge University Press. 241pp.

Schomber, H. W. (1966). Die Verbreitung und der Bestand des zentralafrikanischen Breitmaulnashorn. *Saugetierk. Mitt.*, **14**, 214–27.

Schweger, C. E. (1982). Late Pleistocene vegetation of eastern Beringia: pollen analysis of dated alluvium. In *Paleoecology of Beringia*, ed. D. M. Hopkins, J. V. Matthews Jr., C. E. Schweger & S. B. Young, pp. 95–112. New York: Academic Press.

Scotcher, J. S. B. (1982). Interrelations of vegetation and eland in Giant's Castle Game Reserve, Natal. PhD thesis, University of the Witwatersrand.

Scotcher, J. S. B., Stewart, D. R. M. & Breen, C. M. (1978). The diet of hippopotamus in Ndumu Game Reserve, Natal, as determined by faecal analysis. *S. Afr. J. Wildl. Res.*, **8**, 1–11.

Scott, L. (1984). Palynological evidence for Quarternary paleoenvironments in southern Africa. In *Southern African Prehistory and Paleoenvironments*, ed. R. G. Klein, pp. 65–80. Rotterdam: Balkema.

Selous, F. C. (1899). The white or square-lipped rhinoceros. In *Great and Small Game of Africa*, ed. H. A. Bryden, pp. 52–67. London: Rowland Ward.

Shackleton, N. J., Hall, M. A., Line, J. & Shuxi, Cang (1983). Carbon isotope data in core V19–30 confirm reduced carbon dioxide concentration in the ice age atmosphere. *Nature*, **306**, 319–22.

Sherry, B. J. (1975). Reproduction of elephant in Gonarezhou, South Eastern Rhodesia. *Arnoldia (Rhodesia)*, **7**, 29, 1–13.

Sherry, B. Y. (1978). Growth of elephants in the Gonarezhou National Park, south-eastern Rhodesia. *S. Afr. J. Wildl. Res.*, **8**, 49–58.

Short, J. (1981). Diet and feeding behaviour of the forest elephant. *Mammalia*, **45**, 177–86.

Short, R. V. (1966). Oestrous behaviour, ovulation and the formation of the corpus luteum in the African elephant. *E. Afr. Wildl. J.*, **4**, 56–69.

Shoshani, J. & Eisenberg, J. F. (1982). *Elephas maximus*. Mammalian species No. 182, 8pp. The American Society of Mammalogists.

Sidney, J. (1966). The past and present distribution of some African ungulates. *Trans. Zool. Soc. Lond.*, **30**, 5–397.

Siegfried, W. R. & Davies, B. R. (1982). *Conservation of Ecosystems: Theory and Practice*. S. Afr. Nat. Sci. Progr. Rep. No. 61, Pretoria: CSIR. 97pp.

Sikes, S. K. (1971). *The Natural History of the African Elephant*. London: Weidenfeld & Nicolson, 397pp.

Simpson, C. D. (1968). Reproduction and population structure in the greater kudu in Rhodesia. *J. Wildl. Manage.*, **32**, 149–61.

Simpson, C. D. (1974). Food studies of the Chobe bushbuck. *Arnoldia (Rhodesia)*, **6**, 32, 1–9.

Simpson, G. L. (1980). *Splendid Isolation*. New Haven: Yale University Press.

Sinclair, A. R. E. (1974). The social organisation of the East African buffalo. In *The Behaviour of Ungulates and its Relation to Management*, ed. V. Geist & F. Walther, pp. 676–89. IUCN public., new series no. 24, Morges: IUCN.

Sinclair, A. R. E. (1975). The resource limitation of trophic levels in tropical grassland ecosystems. *J. Anim. Ecol.*, **44**, 497–520.

Sinclair, A. R. E. (1977). *The African Buffalo. A Study of Resource Limitation of Populations*. Chicago: University of Chicago Press. 355pp.

Sinclair, A. R. E. (1983). Management of conservation areas as ecological baseline controls. In *Management of Large Mammals in African Conservation Areas*, ed. R. N. Owen-Smith, pp. 13–22. Pretoria: Haum.

Sinclair, A. R. E. (1985). Does interspecific competition or predation shape the African ungulate community? *J. Anim. Ecol.*, **54**, 899–918.

Sinclair, A. R. E. & Norton-Griffiths, M. (1979). *Serengeti. Dynamics of an Ecosystem*. Chicago: University of Chicago Press. 389pp.

Skinner, J. D., Scorer, J. A. & Millar, R. P. (1975). Observations on the reproductive physiological status of mature herd bulls, bachelor bulls, and young bulls in the hippopotamus. *Gen. Compar. Endocr.*, **26**, 92–5.

Skinner, J. D. & van Zyl, J. H. M. (1969). Reproductive performance of the common eland in two environments. *J. Reprod. Fert. Suppl.*, **6**, 319–22.

Smart, N. O. E., Hatton, J. C. & Spence, D. H. N. (1985). The effect of long-term exclusion of large herbivores on vegetation in Murchison Falls National Park, Uganda. *Biol. Cons.*, **33**, 229–45.

Smith, N. S. & Buss, I. O. (1973). Reproductive ecology of the female African elephant. *J. Wildl. Manage.*, **37,** 524–33.

Smithers, R. H. N. (1971). *The Mammals of Botswana.* Salisbury: Trustees of the National Museums of Rhodesia.

Smithers, R. H. N. (1983). *The Mammals of the Southern African Subregion.* Pretoria: University of Pretoria. 367pp.

Smuts, G. L. (1974). Growth, reproduction and population characteristics of Burchell's zebra in the Kruger National Park. DSc thesis, University of Pretoria.

Smuts, G. L. (1975a). Home range sizes for Burchell's zebra from the Kruger National Park. *Koedoe*, **18**, 139–146.

Smuts, G. L. (1975b). Pre- and post-natal growth phenomena of Burchell's zebra from the Kruger National Park. *Koedoe*, **18**, 69–102.

Smuts, G. L. (1975c). Reproduction and population characteristics of elephants in the Kruger National Park. *J. Sth. Afr. Wildl. Manage. Assoc.*, **5**, 1–10.

Smuts, G. L. (1976). Reproduction in the zebra mare from the Kruger National Park. *Koedoe*, **19**, 89–132.

Smuts, G. L. (1978). Interrelations between predators, prey and their environment. *BioScience*, **28**, 316–20.

Smuts, G. L. (1979). Diet of lions and spotted hyenas assessed from stomach contents. *S. Afr. J. Wildl. Res.*, **9**, 19–25.

Smuts, G. L. & Whyte, I. C. (1981). Relationships between reproduction and environment in the hippopotamus in the Kruger National Park. *Koedoe*, **24**, 169–85.

Sokal, R. R. & Rohlf, F. J. (1969). *Biometry. The Principles and Practice of Statistics in Biological Research.* San Francisco: Freeman. 776pp.

Soule, M. E. (1980). Thresholds for survival; maintaining fitness and evolutionary potential. In *Conservation Biology*, ed. M. E. Soule & B. A. Wilcox, pp. 151–70. Sunderland, Mass: Sinauer.

Sowls, L. K. (1974). Social behaviour of the collared peccary. In *The Behaviour of Ungulates and its Relation to Management*, ed. V. Geist & F. Walther, pp. 144–65. IUCN public., new series no. 24, Morges: IUCN.

Spinage, C. A. (1968). A quantitative study of the daily activity of the Uganda defassa waterbuck. *J. Zool. Lond.*, **159**, 329–61.

Spinage, C. A. (1969). Naturalistic observations on the reproductive and material behaviour of the Uganda defassa waterbuck. *Z. Tierpsychol.*, **26**, 39–47.

Spinage, C. A. (1970). Population dynamics of the Uganda defassa waterbuck in the Queen Elizabeth Park, Uganda. *J. Anim. Ecol.*, **39**, 51–78.

Spinage, C. A. (1973). A review of ivory exploitation and elephant population trends in Africa. *E. Afr. Wildl. J.*, **11**, 281–9.

Spinage, C. A. (1974). Territoriality and population regulation in the Uganda defassa waterbuck. In *The Behaviour of Ungulates and its Relation to Management*, ed. V. Geist & F. Walther, pp. 635–43. IUCN public., new series no. 24, Morges: IUCN.

Spinage, C. A. (1982). *A Territorial Antelope. The Uganda Waterbuck.* London: Academic Press. 334pp.

Spinage, C. A., Guinness, F., Eltringham, S. K. & Woodford, M. H. (1972). Estimation of large mammal numbers in the Akagera National Park and Mutara Hunting Area, Rwanda. *Terre et Vie*, **4**, 561–70.

Stanley-Price, M. R. (1974). The feeding ecology of Coke's hartebeest in Kenya. PhD thesis, University of Oxford.

Stanley-Price, M. R. (1977). The estimation of food intake, and its seasonal variation, in the hartebeest. *E. Afr. Wild. J.*, **15**, 107–24.

Steadman, D. W. & Martin, P. S. (1984). Extinctions of birds in the late Pleistocene of North America. In *Quaternary Extinctions*, ed. P. S. Martin & R. G. Klein, p. 466–77. Tucson: University of Arizona Press.

Steele, N. (1968). *Game Ranger on Horseback.* Cape Town: Books of Africa.

Stewart, D. R. M. & Zaphiro, D. R. P. (1963). Biomass and density of wild herbivores in different East African habitats. *Mammalia*, **27**, 483–96.

Struhsaker, T. T. (1967). Behaviour of elk during the rut. *Z. Tierpsychol.*, **24**, 80–114.

Swanepoel, C. M. & Swanepoel, S. M. (1986). Baobab damage by elephant in the middle Zambezi Valley, Zimbabwe, *Afr. J. Ecol.*, **24**, 129–32.

Talbot, L. M. & Talbot, M. H. (1963a). The wildebeest in western Masailand, East Africa. *Wild Monogr.* No. 12, 88pp.

Talbot, L. M. & Talbot, M. H. (1963b). The high biomass of wild ungulates on East African savanna. *Trans. 28th N. Amer. Wildl. Conf.*, pp. 465–76.

Taylor, C. R. (1973). Energy cost of animal locomotion. In *Comparative Physiology*, ed. L. Bolis, K. Schmidt-Nielsen & S. H. P. Maddrell, pp. 23–42. New York: New Holland.

Taylor, C. R. & Maloiy, G. M. O. (1967). The effect of dehydration and heat stress on intake and digestion of food in some East African bovids. *Trans. 8th Int. Congr. Game Biol.*

Taylor, L. R. & Taylor, R. A. J. (1977). Aggregation, migration and population mechanics. *Nature*, **265**, 415–21.

Taylor, R. A. J. (1981a). The behavioural basis of redistribution. I The delta-model concept. *J. Anim. Ecol.*, **50**, 573–86.

Taylor, R. A. J. (1981b). The behavioural basis of redistribution. II Simulations of the delta-model. *J. Anim. Ecol.*, **50**, 587–604.

Thenius, E. (1968). Nashorner. In *Grzimek's Tierleben*, ed. B. Grzimek, XIII Saugetiere 4.

Thenius, E. (1969). Stammegesichte der Saugetiere. Ceratomorpha II (Rhinocerotoidea). *Handbuch der Zoologie*, **8**, 2, 543–54.

Thompson, P. J. (1975). The role of elephants, fire and other agents in the decline of a *Brachystegia boehmii* woodland. *J. Sth. Afr. Wildl. Mgmt. Ass.*, **5**, 11–18.

Thomson, B. R. (1973). Wild reindeer activity. Hardangervidda 1971. Mimeogr. Rep., Statens Vildundersohelse, Direktoratet for Jakt, Vilstell og Ferskvannsfiske, and International Biological Programme (Norway IBP, PT/UM), Trondheim.

Thonney, M. L., Touchberry, R. W., Goodrich, R. D., & Meicke, J. C. (1976). *J. Anim. Sci.*, **43**, 692–704.

Thorbahn, P. F. (1984). Br'er elephant and the briar patch. *Natural History (N. Y.)*, **93**, 70–81.

Thornton, D. D. (1971). The effect of complete removal of hippopotamus on grassland in the Queen Elizabeth National Park, Uganda. *E. Afr. Wildl. J.*, **9**, 47–55.

Trivers, R. L. & Willard, D. E. (1973). Natural selection of parental ability to vary the sex ratio of offspring. *Science*, **179**, 90–2.

Trotter, M. M. & McCulloch, B. (1984). Moas, men and middens. In *Quaternary Extinctions*, ed. P. S. Martin & R. G. Klein, pp. 708–27. Tucson: University of Arizona Press.

Turner, M., & Watson, M. (1964). A census of game in Ngorongoro Crater. *E. Afr. Wildl. J.*, **2** 165–8.

Tyrrell, J. G. (1985). Distribution of elephants in the Tsavo region during the late 19th century. *E. Afr. Wildl. J.*, **23**, 29–33.

Ullrich. W. (1964). Zur biologie der Panzerhashorner in Assam. *D. Zool. Garten.*, *NF*, **21**, 129–51.

Vancuylenberg, B. W. B. (1977). Feeding behaviour of the Asiatic elephant in south-east Sri Lanka in relation to conservation. *Biol. Cons.*, **12**, 33–54.

van Gyseghem, R. (1984). Observations on the ecology and behaviour of the northern white rhinoceros. *Z. Saugetierk*, **49**, 348–58.

van Hoven, W. (1977). Stomach fermentation rate in the hippopotamus. *S. Afr. J. Sci.*, **73**, 216.

van Hoven, W. (1978). Digestive physiology in the stomach complex and hindgut of the hippopotamus. *S. Afr. J. Wildl. Res.*, **8**, 59–64.

van Hoven, W., Prins, R. A. & Lankhorst, A. (1981). Fermentative digestion of the African elephant. *S. Afr. J. Wild. Res.*, **11** 78–86.

van Jaarsveld, A. S. & Knight-Eloff, A. K. (1984). Digestion in the porcupine. *S. Afr. J. Zool*, **19**, 109–112.

Van Lavieren, L. P. & Esser, J. D. (1980). Numbers, distribution and habitat preference of large mammals in Bouba Njida National Park, Cameroon. *Afr. J. Ecol.*, **18**, 141–53.

van Wyk, P. & Fairall, N. (1969). The influence of the African elephant on the vegetation of the Kruger National Park. *Koedoe*, **12**, 57–89.

van Zyl, J. H. M. & Skinner, J. D. (1970). Growth and development of the springbok foetus. *Afr. Wild Life*, **24**, 309–16.

Venter, J. (1979). The ecology of the southern reedbuck on the eastern shores of Lake St. Lucia, Zululand, MSc thesis, University of Natal.

Vereshchagin, N.K. (1967). Primitive hunters and Pleistocene extinctions in the Soviet Union. In *Pleistocene Extinctions*, ed. P. S. Martin & H. E. Wright, pp. 365–98. New Haven: Yale University Press.

Vereshschagin, N. K. & Baryshnikov, G. T. (1984). Quarternary mammalian extinctions in northern Eurasia. In *Quaternary Extinctions*, ed. P. S. Martin & R. G. Klein, pp. 483–516. Tucson: University of Arizona Press.

Verheyen, R. (1954). *Monographic Ethologique de la Hippopotame*. Bruxelles: Inst. des Parcs Nat. du Congo Belge. 91pp.

Verme, L. J. (1983). Sex ratio variation in *Odocoileus*: a critical review. *J. Wildl. Manage.*, **47**, 573–82.

Verme, L. J. & Ozaga, J. J. (1981). Sex ratio of white-tailed deer and the estrous cycle. *J. Wildl. Manage.*, **45**, 710–5.

Vesey-Fitzgerald, D. F. (1960). Grazing succession among East African game animals. *J. Mammal.*, **41**, 161–72.

Vesey-Fitzgerald, D. F. (1973). Animal impact on vegetation and plant succession in Lake Manyara National Park, Tanzania. *Oikos*, **24**, 314–25.

Vesey-Fitzgerald, D. F. (1974). The changing state of *Acacia xanthophloea* groves in Arusha National Park, Tanzania. *Biol. Cons.*, **6**, 40–7.

Viljoen, P. C. (1980). Distribution and numbers of the hippopotamus in the Olifants and Blyde Rivers. *S. Afr. J. Wildl. Res.*, **10**, 129–32.

Vincent, J. (1969). The status of the square-lipped rhinoceros in Zululand. *Lammergeyer (Natal)*, **10**, 12–21.

Vincent, J. (1970). The history of Umfolozi Game Reserve, Zululand. *Lammergeyer (Natal)*, **11**, 7–48.

Volman, T. P. (1984). Early prehistory of southern Africa. In *Southern African Prehistory and Paleoenvironments*, ed. R. G. Klein, pp. 169–220. Rotterdam: Balkema.

Von Ketelholdt, H. F. (1977). The lambing interval of the blue duiker in captivity, with observations on its breeding and care. *S. Afr. J. Wildl. Res.*, **7**, 41–3.

Von Richter, W. (1971). *The Black Wildebeest*. O F.S. Prov. Admin., Nature Conserv. Misc. Rep. No. 2.

Von Richter, W. (1972). Territorial behaviour of the black wildebeest. *Zoologica Africana*, **7**, 207–31.

Vrba, E. S. (1985). African Bovidae: evolutionary events since the Miocene. *S. Afr. J. Sci.*, **81**, 263–6.

Waldo, D. R., Smith, L. W. & Cox, E. L. (1972). Model of cellulose disappearance from the rumen. *J. Dairy Science*, **55**, 125–8.

Walker, B. H., Emslie, R. H., Owen-Smith, N. & Scholes, R. J. (1987). To cull or not to cull: lessons from a southern African drought. *J. Appl. Ecol.* **24**, 381–401.

Walker, B. H. & Goodman, P. S. (1983). Some implications of ecosystem properties for wildlife management. In *Management of Large Mammals in African Conservation Areas*, ed. R. N. Owen-Smith, pp. 79–92. Pretoria: Haum.

Walther, F. R. (1964). Einige Verhaltensbeobachtungen an Thomson-gazelle im Ngorongoro-Krater. *Z. Tierpsychol.*, **21**, 871–90.

Walther, F. R. (1965). Verhaltensstudien an der Grantsgazelle. *Z. Tierpsychol*, **22**, 167–208.

Walther, F. R. (1972a). Territorial behaviour in certain horned ungulates, with special reference to the examples of Thomson's and Grant's gazelles. *Zoologica Africana*, **7**, 303–8.

Walther, F. R. (1972b). Social grouping in Grants gazelle in the Serengeti National Park. *Z. Tierpsychol.*, **31**, 348–403.

Walther, F. R. (1973). Round the clock activity of Thomsons gazelle in the Serengeti National Park. *Z. Tierpsychol.*, **32**, 75–105.

Walther, F. R. (1978). Behavioural observations on oryx antelope invading Serengeti National Park, Tanzania. *J. Mammal.*, **59**, 243–60.

Waltz, E. C. (1982). Alternative mating tactics and the law of diminishing returns: the satellite threshold model. *Behav. Ecol. Sociobiol.*, **10**, 75–83.

Waser, P. M. (1974). Spatial associations and social interactions in a solitary antelope: the bushbuck. *Z. Tierpsychol.*, **37**, 24–36.

Waser, P. M. (1975). Diurnal and nocturnal strategies of the bushbuck. *E. Afr. Wildl. J.*, **13**, 49–64.

Watson, R. M. (1969). Reproduction of wildebeest in the Serengeti region, and its significance to conservation. *J. Reprod. Fert. Suppl.* **6**, 287–310.

Weatherhead, P. J. (1984). Mate choice in avian polygyny: why do females prefer older males? *Am. Nat.*, **123**, 873–5.

Webb, S. D. (1984). Ten million years of mammalian extinctions in North America. In *Quaternary Extinctions*, ed. P. S. Martin & R. G. Klein, pp. 189–210. Tucson: University of Arizona Press.

Weir, J. S. (1972). Spatial distribution of elephants in an African national park in relation to environmental sodium. *Oikos*, **23**, 1–13.

Weir, J. & Davison, E. (1965). Daily occurrence of African game animals at waterholes during dry weather. *Zoologica Africana*, **1**, 353–68.

West, F. H. (1984). The antiquity of man in America. In *Late-Quaternary Environments of the United States.* ed., H. E. Wright, Jr., Vol. 1. The Late Pleistocene, ed. S. C. Porter, pp. 364–82. Minneapolis: University of Minnesota Press.

Western, D. (1975). Water availability and its influence on the structure and dynamics of a savannah large mammal community. *E. Afr. Wildl. J.*, **13**, 265–86.

Western, D. (1979). Size, life history and ecology in mammals. *Afr. J. Ecol.*, **17**, 185–204.

Western, D. & Lindsay, W. K. (1984). Seasonal herd dynamics of a savanna elephant population. *Afr. J. Ecol.*, **22**, 229–44.

Western, D. & Sindiyo, D. M. (1972). The status of the Amboseli rhino population. *E. Afr. Wildl. J.*, **10**, 43–57.

Western, D. & Van Praet, C. (1973). Cyclical changes in the habitat and climate of an East African ecosystem. *Nature*, **241**, 104–6.

Weyerhaeuser, F. J. (1985). Survey of elephant damage to baobabs in Tanzania's Lake Manyara National Park. *Afr. J. Ecol.*, **23**, 235–43.

Wiley, R. H. (1974). Evolution of social organization and life history patterns among grouse. *Q. Rev. Biol.*, **49**, 201–27.

Williamson, B. R. (1975a). Seasonal distribution of elephant in Wankie National Park. *Arnoldia (Rhodesia)*, **7**, 11, 1–16.

Williamson, B. R. (1975b). The condition and nutrition of elephant in Wankie National Park. *Arnoldia (Rhodesia)*, **7**, 12, 1–20.

Williamson, B. R. (1976). Reproduction in female African elephant in the Wankie National Park, Rhodesia. *S. Afr. J. Wildl. Res.*, **6**, 89–93.

Wilson, E. O. (1975). *Sociobiology. The New Synthesis.* Cambridge, Mass.: Harvard University Press. 697pp.

Wilson, V. J. (1966). Observations on Lichtenstein's hartebeest over a three year period, and their response to various tsetse control measures in E. Zambia. *Arnoldia (Rhodesia)*, **2**, 15, 1–14.

Wilson, V. J. (1968). Weights of some mammals from Eastern Zambia. *Arnoldia (Rhodesia)*, **3**, 1–19.

Wilson, V. J. (1969a). Eland in eastern Zambia. *Arnoldia (Rhodesia)* **4**, 12, 1–9.

Wilson, V. J. (1969b). The large mammals of the Matopos National Park. *Arnoldia (Rhodesia)*, **4**, 13, 1–32.

Wilson, V. J. & Child, G. F. T. (1964). Notes on bushbuck from a tsetse fly control area in Northern Rhodesia. *Puku*, **2**, 118–28.

Wilson, V. J. & Child, G. (1965). Notes on klipsinger from tsetse fly control areas in eastern Zambia. *Arnoldia (Rhodesia)*, **1**, 35, 1–9.

Wilson, V. J. & Clarke, J. E. (1962). Observations on the common duiker based on material collected from a tsetse control game elimination scheme. *Proc. Zool. Soc. Lond.*, **138**, 487–97.

Wilson, V. J. & Kerr, M. A. (1969). Brief notes on reproduction in steenbok. *Arnoldia (Rhodesia)*, **4**, 23, 1–5.

Wing, L. D. & Buss, I. O. (1970). Elephants and forests. *Wildl. Monogr.* No. 19, 92pp.

Wirtz, P. (1981). Territorial defence and territory takeover by satellite males in the waterbuck. *Behav. Ecol. Sociobiol.*, **8**, 161–2.

Wirtz, P. (1982). Territory holders, satellite males and bachelor males in a high density population of waterbuck and their association with conspecifics. *Z. Tierpsychol.*, **58**, 277–300.

Wittenberger, J. F. (1980). Group size and polygamy in social mammals. *Am. Nat.*, **115**, 197–222.

Wolff, J. O. (1980). The role of habitat patchiness in the population dynamics of snowshoe hares. *Ecol. Monogr.*, **50**, 111–30.

Work, D. R. (1986). Summary report of aerial surveys conducted in 1983, 1984 and 1985. Unpublished report, Resource Ecology Group, University of the Witwatersrand.

Wright, H. E. Jr. (1977). Quaternary vegetation history – some comparisons between Europe and America. *Ann. Rev. Earth Planet. Sci.*, **5**, 123–58.

Wright, H. E. Jr. (ed.) (1984). *Late-Quaternary Environments of the United States.* Vol. 1. The Late Pleistocene. Minneapolis: University of Minnesota Press.

Wyatt, J. R. & Eltringham, S. K. (1974). The daily activity of the elephant in the Rwenzori National Park, Uganda. *E. Afr. Wildl. J.*, **12**, 273–90.

Yoaciel, S. M. (1981). Change in the populations of large herbivores and in the vegetation community in Mweya Peninsula, Rwenzori National Park, Uganda. *Afr. J. Ecol.*, **19**, 303–12.

Yurtsev, B. A. (1982). Relicts of the xerophyte vegetation of Beringia in northeastern Asia. In *Paleoecology of Beringia*, ed. D. M. Hopkins, J. V. Matthews, C. E. Schweger & S. B. Young, pp. 157–78. New York: Academic Press.

Zahavi, A. (1975). Mate selection – a selection for a handicap. *J. Theor. Biol.*, **53**, 205–14.

Zimmerman, I. (1978). The feeding ecology of Africander steers on mixed bushveld at Nylsvley Nature Reserve, Transvaal. MSc thesis, University of Pretoria.

Index