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Editors

The Ecology of Browsing and Grazing

Chapter 11
Managing Large Herbivores in Theory and Practice: Is the Game the Same for Browsing and Grazing Species?

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11.1   Introduction

Management of large wild herbivores sometimes includes action on the availability of resources and/or on the abundance of predators, but the management of most populations of these animals is limited to the choice of hunting quotas (Williams et al. 2002). The dynamics of the target populations, in interaction with their habitats, is therefore a central process in management. The dynamics of populations is driven by their demographic parameters, i.e., the rates of reproduction and survival. Demographic rates vary according to the sex and age of the individuals, and also show different degrees of temporal and spatial variation among populations (Gaillard et al. 2000; Coulson et al. 2001). In this chapter we first address the question: do browsing and grazing large herbivores have different demographic rates driving the dynamics of their populations?

Management of most populations of large herbivores being, as stated, based on the choice of quotas for offtake by hunting, a reliable assessment of trends in population size is required. Total counts of individuals in the whole population area or sample counts of plots/transects have been the most popular way for assessing population sizes (e.g., Caughley 1977; Seber 1982; for deer see Cederlund et al. 1998 and for mountain ungulates Loison et al. 2006). In the context of game species such as these, hunting-related methods such as drives (McCullough 1979), observations from vantage points (Ratcliffe 1987), and number of animals seen during hunts (Ericsson and Wallin 1999) are often used. However, such counts are often imprecise, and biased (Williams et al. 2002). Caughley (1977) pointed out that it is difficult to achieve a coefficient of variation of less than 20% for counts of animals. The roe deer (*Capreolus capreolus*), the most abundant deer species in Europe (Andersen et al. 1998), is particularly difficult to count and underestimates of density can be as high as 50% (Cederlund et al. 1998). Since grazers and browsers live in different habitats (Jarman 1974), they pose different problems in estimation of trends in abundance, due in particular to differences in visibility between habitats and to differences in variance because of contrasting group sizes.

Another problem in the management of large herbivores is that the response of populations to a given offtake varies according to the relative importance of

density-dependent and density-independent processes acting on the population (Caughley 1977). Populations of animals in good condition (because resources are abundant) respond differently from populations of animals in poor condition to the same offtake (Caughley 1977). Monitoring populations of large herbivores should, therefore, be rooted in the concept of density dependence, the functional dependence of a demographic rate on changes in population size (Williams et al. 2002). This provides a measure of the population–environment relationships, as illustrated in Fig. 11.1. Density dependence is a commonly observed process in populations of large herbivores (Saether 1997; Gaillard et al. 2000). It is widely accepted that populations of large herbivores vary in numbers according to a generalized logistic model (also called theta logistic model; Lande et al. 2003) that includes non-linear density-dependent changes in population growth (Gilpin and Ayala 1973; Fowler 1981). At very low density, the population shows a 'colonising' status and the growth rate is close to maximal (r-max sensu Caughley 1977). The population's productivity is, however, quite low because of the small size of the population. As the size of the population increases, small decreases in individual performance lead the growth rate of the population to decrease slowly, while the population productivity increases. When the population size reaches 50–90% (depending on the generation time, Fowler 1988) of the carrying capacity (defined here as the population size at which the population no longer increases), the population productivity peaks (MSY—maximum sustainable yield—in Caughley 1977). After this point, the
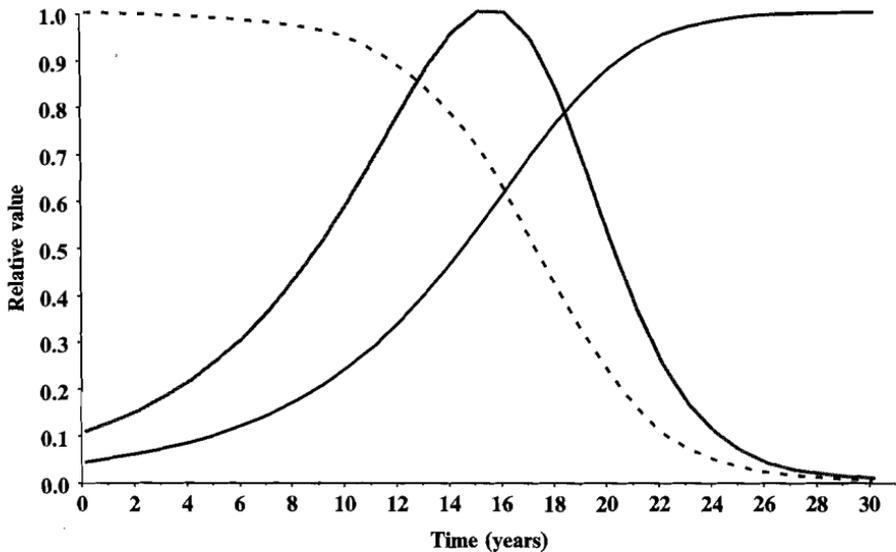
Fig. 11.1 Growth, individual growth and size of a theoretical population according to a theta logistic model. The *black full line* corresponds to changes of the population size over time, the *grey full line* corresponds to the variation of the population productivity according to the population size, and the *dotted line* corresponds to the variation of the individual performance according to the population size

performance of the individuals decreases markedly with declining body condition at high population density, and the productivity of the population declines, too. The demographic status of the population is then close to saturation. The pattern described here can happen at very different absolute densities in different areas because population density relative to habitat quality, rather than to absolute density, influences life-history traits (Van Horne 1983).

Populations of large herbivores have increased tremendously in the temperate countries (Gill 1990) and high-density populations are now widespread (McShea et al. 1997; Warren 1997). Their management, therefore, requires knowledge of the relationships between the animals and their resources as well as an assessment of the size of the population.

We show that a set of ecological indicators of the temporal changes in abundance and of the relationships between the population and the habitat can be a reliable basis for monitoring. This approach has been developed independently in France for the roe deer, and for other large herbivores in other countries (du Toit 2002). We address the issue of whether the same methods of monitoring and management are appropriate for grazers and browsers in Sects. 11.3 Monitoring, and 11.4 Management.

11.2 The Dynamics of Grazer and Browser Populations

Several recent papers have described differences in biological traits among feeding types in large herbivores. From these, Gordon (2003) concluded there is little substantive evidence for differences in morphology and physiology between feeding types once body mass has been accounted for. However, most previous comparative studies of grazers and browsers have dealt with morphology and physiology, and very few have focussed on life-history traits (but see Saether and Gordon 1994 for a notable exception). According to the life history theory (Stearns 1992), life history tactics of vertebrates range along a fast-slow continuum involving the association between relatively large reproductive output, short lifespan, and early age at first reproduction (see Stearns 1983 on mammals, Gaillard et al. 1989 on mammals and birds, Shine and Charnov 1992 on reptiles, Rochet et al. 2000 on fishes). We aim to test whether grazers and browsers have different positions on this fast-slow continuum using published demographic data. We focussed on the reproductive traits (age at first reproduction and litter size), adult survival, and on generation time, which latter provides a direct measure of the speediness of life history (Gaillard et al. 2005). We did not include juvenile survival because juvenile survival varies greatly among both years within populations and populations within a given species (see Gaillard et al. 1998a, 2000 for reviews), so that a large number of possible confounding effects would need to be accounted for to get a reliable comparison among the survival of juveniles of the different feeding types. Although the influence of phylogeny has been discussed in the context of comparisons between grazers and browsers (see, e.g., Perez-Barberia and Gordon 2000 versus

Mysterud 1998), we did not analyse phylogenetic influences. The usefulness of correcting for phylogenetic inertia has been challenged (e.g., Price 1997; Ricklefs and Starck 1996), leading many authors to perform both a standard analysis using the raw data and a comparative analysis accounting for phylogenetic inertia (independent contrasts in most cases; see Fisher and Owens 2000; Nagy and Bradshaw 2000; Perez-Barberia and Gordon 2001 for examples). As the correction for phylogenetic inertia increases the p-values of the statistical tests, but does not affect the parameter estimates, we will consider the size of the effects more than the significance of the statistical tests. To test for life-history differences among feeding types, we split the species of large herbivores into three categories of feeding types: browsers with a diet including less than 10% grass, intermediate feeders with a diet including between 10 and 90% grass, and grazers with a diet of more than 90% of grass; in agreement with most recent analyses focussing on feeding types (e.g., Van Wieren 1996; Perez-Barberia and Gordon 2000). We used available data bases (restricted to ruminant species) to assess the influence of feeding types on life history traits. To account for the marked allometric relationships that occur in most life history traits (Peters 1983; Calder 1984; Brown and West 2000), we performed an ANCOVA with the log-transformed life history trait as the dependent variable, the species-specific body mass (after log-transformation) as the covariate, and the feeding type as the factor. We ran five models in each case: (1) the model including an interaction term between feeding types and body mass that corresponds to different allometric relationships among feeding types; (2) the model including an additive effect between feeding types and body mass that corresponds to a similar allometric relationship, but with differences in the life history trait at a given mass among feeding types; (3) the model including the allometric relationship only (i.e., no influence of feeding types); (4) the model including differences among feeding types only (i.e., no influence of body mass); and (5) the model including a constant value of the life history trait (i.e., no influence of feeding types or body mass). According to the recommendations of Burnham and Anderson (1998), we used the model with the lowest Akaiké Information Criterion (AIC) as the best model (best compromise between precision and accuracy).

Differences in reproductive traits among feeding types. We used the species-specific data available in Van Wieren (1996) to assess the influence of feeding types on age at first breeding (first recorded matings, $N = 140$ species) and on fecundity ($N = 141$), principally bovids and cervids from a wide variety of habitats in Africa, Eurasia, and the Americas. For age at first breeding, the best model included additive effects of body mass and feeding types (Table 11.1). As expected, the age at first breeding was allometrically related to body mass, although the slope was much less than the expected value of 0.25 for biological time (slope 0.147, $SE = 0.019$). For a given body mass browsers bred for the first time earlier than intermediate feeders (difference 0.269, $SE = 0.058$) and grazers (difference 0.349, $SE = 0.066$). The additive effects of body mass and feeding types accounted for 61.8% of the variability observed in age at first breeding. For the fecundity (measured as the number of offspring produced per year), the same model was retained (Table 11.1). As expected, fecundity decreased allometrically with increasing body mass

Table 11.1 Model selection for the analysis of the variation in some life history traits. The table reports the AIC value of each model fitted (1: Interactive effects between feeding type and body mass, 2: additive effects of feeding type and body mass, 3: effect of body mass (allometric effect), 4: effect of feeding type, 5: constant value for the life history trait). The selected model (lowest AIC value) occurs in *italics*

Model Life history trait	1	2	3	4	5
Age at first breeding	30.61	*27.63*	53.99	74.79	156.41
Fecundity	90.43	*86.57*	88.86	111.73	146.45
Adult survival	49.58	45.84	44.27	43.86	*42.27*
Generation time	11.28	*7.98*	8.33	23.36	20.18

although the slope differed from −0.25, the expected allometric exponent for frequency (slope −0.130, SE=0.024). For a given body mass browsers tended to have higher fecundity than intermediate feeders (difference 0.095, SE=0.072) and had higher fecundity than grazers (difference 0.202, SE=0.081). The additive effects of body mass and feeding types accounted for 37.5% of the variability observed in annual fecundity.

Differences in adult survival among feeding types. We used the species-specific data available in Gaillard et al. (2000) to assess the influence of feeding types on adult survival (N=24 species). The model with a constant adult survival (2.42, SE=0.11 on a logit scale corresponding to a survival rate of 0.92) was selected (Table 11.1). The additive effects of body mass and feeding types only accounted for 9.63% of the variability observed in adult survival.

Differences in generation time among feeding types. We used the data in Sinclair (1996) and Gaillard et al. (2000) to assess the influence of feeding types on generation time (N=26 species). The best model included additive effects of body mass and feeding types (Table 11.1). As expected, the generation time was allometrically related to body mass, with a slope very close to the expected value of 0.25 for biological times (slope 0.227, SE=0.050). For a given body mass browsers had shorter generation time than intermediate feeders (difference 0.251, SE=0.132) and grazers (difference 0.223, SE=0.134). The additive effects of body mass and feeding types accounted for 50.4% of the variability observed in generation time (Fig. 11.2).

These analyses show that browsers have faster life histories for a given body mass than intermediate feeders and grazers. A faster life history can involve an earlier age at first breeding, a higher fecundity rate, and/or a shorter lifespan: we show that browsers have faster life histories than grazers and intermediate feeders because they breed earlier and produce more offspring. Thus, a 100 kg browser breeds for the first time at 1.15 years of age and produces an average of 1.37 offspring/year, whereas a grazer of the same mass breeds for the first time at 1.62 years of age and produce an average of 1.12 offspring/year (see Table 11.2). As expected from scaling theory (Brown and West 2000), the reproductive output of large herbivores decreased with increasing body mass at similar rates in all feeding types (Table 11.2). Adult survival of large herbivores, on the other hand, was quite constant at 0.92 and did not depend either on body mass or on feeding type. Such a constancy of adult survival fits with previous analyses of large herbivores that
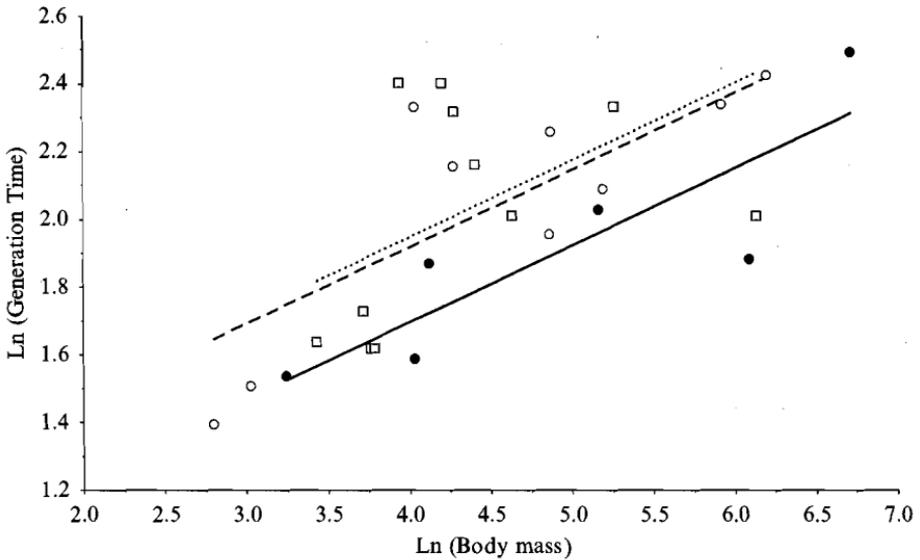
Fig. 11.2 Allometric relationship between generation time and body mass in ruminants in relation to the feeding type. The *lines* (*full line* for browsers, *dashed line* for intermediate feeders, and *dotted line* for grazers) that correspond to the selected model (i.e., additive effects of body mass and feeding types) and the data points (*filled circles* for browsers, *open squares* for intermediate feeders, and *open circles* for grazers) are shown

Table 11.2 Expected age at first breeding (AFB, in years) and annual fecundity (Fec, in number of offspring born) for large herbivores of different body mass and belonging to different feeding types. The estimates correspond to the models selected in each analysis (see text for further details)

	Browsers		Intermediate feeders		Grazers	
	AFB	Fec	AFB	Fec	AFB	Fec
25 kg	0.934	1.636	1.222	1.488	1.324	1.337
50 kg	1.034	1.495	1.353	1.360	1.466	1.222
100 kg	1.145	1.367	1.498	1.243	1.623	1.117
500 kg	1.451	1.109	1.898	1.008	2.056	0.906

reported high survival rates resilient to environmental variations (Gaillard et al. 2000; Gaillard and Yoccoz 2003). The shorter generation time of browsers compared to intermediate feeders and grazers is thus due only to a higher reproductive output. While this shorter generation time we report for browsers increases the relative influence of reproductive traits on population growth rate (Gaillard et al. 2005), our analyses demonstrate the existence of a single general demographic pattern common to all large herbivores. Indeed, a 2 kg browser is the fastest large herbivore, in terms of its demography, that can exist. For such an animal, the expected generation time estimated from our selected model is 2.57 years. According to the direct mathematical link that relates elasticities of demographic parameters (i.e., the relative potential impact of demographic parameters on

population growth) and generation time (see Lebreton and Clobert 1991, Gaillard et al. 2005), any population with a generation time longer than 2 years will be more sensitive to a given change in adult survival than to the same change in recruitment. This means that the population growth of all large herbivores, independently of size and feeding type, must be more sensitive to a given change in adult survival than to the same change in a reproductive rate.

The physiological mechanisms behind this difference in generation time remain to be elucidated: the meta-analyses that have so far been conducted do not prove that the digestive ability of browsers is greater than grazers and intermediate feeders, and it is not established that selective feeding by browsers on plants with high levels of cell contents provides them with richer diets (higher protein contents and/or lower cell-wall constituents; Duncan, A. and Poppi, this volume). However, the quality of the data is not good enough to rule out these possible mechanisms.

The life-history differences between browsers and other feeding categories we report here are likely to have general consequences for the status of populations of large herbivores in the future, in the context of global change. The marked increases in CO_2 concentrations (IPCC 2001) may favour woody plants within savannas (Bond and Midgley 2000), so browsers may increase relative to large herbivores with other feeding types in this habitat (see Janis et al. 2000 and Gordon and Prins this volume). However, climate change will not affect the CO_2 concentrations alone, and may decrease the area of savannas, so that the loss of favourable habitat may overcompensate the benefit of increased CO_2 concentrations. On the other hand, the increase of woodland areas in western Europe should benefit browsers. The success of roe deer (Andersen et al. 1998) is consistent with this view. With a faster turnover, browsers should be more resilient to overhunting than grazers and intermediate feeders. A comparative analysis of hunting bags over a large geographical scale in relation to feeding types would be required to test for such a prediction. Lastly, the faster turnover of browsers as compared to large herbivores of other feeding types may confer browsers faster speciation rates. Vrba (1987) has identified some links between ecological features and speciation rates that could indicate that such differences between browsers and grazers could occur; this prediction, however, requires testing explicitly.

11.3   Monitoring

The relationships between the animals and their habitats should be monitored on the basis of 'indicators of ecological change' (sensu Cederlund et al. 1998). As defined by Waller and Alverson (1997), these are 'efficient and reliable indicators capable of serving as "early warnings signs" of impending ecological change' (see also Cairns et al. 1993). Such indicators include measures of trends in abundance of the condition of the animals and of the quality of their habitats. Dale and Beyeler (2001) have reviewed all criteria that an ecological indicator should meet: 'be easily measured, be sensitive to stresses on the system, respond to stress in a predictable

manner, be anticipatory, predict changes that can be averted by management actions, be integrative, have a known response to disturbances, anthropogenic stresses, and changes over time, and have low variability in response'.

As no single indicator fulfils all these criteria, a manageably small set of indicators needs to be derived that, together, meet these criteria (Dale and Beyeler, 2001). Moreover, because we cannot possibly monitor every component of an ecological system, we are constrained to identify a small number of indicators that characterise the relevant parts of the system.

Monitoring the abundance of grazers and browsers. The concepts outlined above are equally valid for grazers and browsers. However, large herbivores of different feeding types live in different habitats (Hofmann 1989; Fritz and Loison 2006), where visibility is different. Grazers typically live in open areas that have less variable, and overall greater, visibility than the often quite closed areas such as forests where browsers live. This means that undercounting might be less of a problem, and bias error might be lower in counts of grazers as compared to browsers. However, this does not mean that total counts of grazers are reliable. For instance, both the number of ibex *Capra ibex* (Gaillard et al. 2003) and chamois *Rupicapra rupicapra* (Loison et al. 2006) counted in open mountainous areas, and the number of African ungulates counted from the air in savanna (Jachmann 2002) have been reported to be severely underestimated. However, the rate of underestimation when counting grazers should be less than that when counting browsers. For instance, an underestimation by a factor of 3 or more has been commonly reported for roe deer (Andersen 1953).

As a corollary of differences in habitat openness, group sizes also differ among feeding types (Jarman 1974), with browsers living in smaller groups than grazers (Fritz and Loison 2006). As the variance of abundance estimate increases with increasing group size (Burnham et al. 1980), the precision of counts, all other things being equal, should be better for browsers than for grazers.

As visibility and group size differ markedly among feeding types and strongly influence the sampling design of population counts, the methods used to monitor trends in the abundance of browsers and grazers should be different.

For browsers like roe deer, the Kilometric Index (measured as the number of animals observed per km of foot transect; Vincent et al. 1991) is closely correlated with true changes in the abundance of deer (as assessed by using Capture-Mark-Recapture methods; see Gaillard et al. 1993) in two forests where the exploitation of trees for timber caused considerable changes in visibility over 20 years. The passage of hurricane Lothar in late 1999 led to the breaking or uprooting of a third of the trees in these forests: there may have been an effect of lower visibility on the index in the three years after the hurricane, but this did not cause any bias in the long term. Visibility that varies spatially is not a major problem, provided that the mean value remains reasonably constant over time. This approach is now widely used for browsers (Maillard et al. 1999). If measures of absolute densities are required, 'distance' methods are insensitive to changes in visibility of the animals (Burnham et al. 1980), as the distances at which they are sighted are taken into account.

For grazers, total or sample counts (most often aerial counts; Jachmann 2001) are usually performed. Although they can provide data for detailed demographic analyses (Owen-Smith and Mason 2005; Owen-Smith and Mills 2006), the accuracy of these procedures has not yet been assessed. However, available empirical evidence indicates that size (larger is better) and colour (high contrast between coat colour and ground colour is better) influence the reliability of aerial counts of large herbivores (Redfern et al. 2002; Jachmann 2002).

Monitoring the condition of grazers and browsers. The phenotypic quality of individuals varies strongly with population density (Fowler 1987), and hence offers a potential tool to monitor the population status of large herbivores. For instance, the body mass of fawns in winter (Vincent et al. 1995; Gaillard et al. 1996), the cohort jaw length (Hewison et al. 1996), and the hind foot length of fawns (Toïgo et al. 2006; Zanneïse et al. 2007) have all been reported to decrease markedly with increasing population density of roe deer and are now used as indicators of population changes in a management context (e.g., Blant and Gaillard 2004 in Switzerland). The winter body mass of fawns is widely used as a short-term measure, since this is related to events (such as rainfall) in the previous summer, and the amount of acorn mast in autumn (Kjellander et al. 2006). The length of the hind foot of fawns integrates events over a longer time-scale, and is very convenient to measure. For longer time horizons the jaw length is a useful index of the quality of individuals (Hewison et al. 1996). Resource shortage in early life leads to permanent effects on the size of many mammals, including red deer *Cervus elaphus* (Mysterud et al. 2002) and roe deer (Pettorelli et al. 2002). This causes variation in performance among year classes and thus to delayed density-dependent effects on the dynamics of their populations ('cohort variation'; Albon et al. 1987).

The reproductive performance of individuals in the population can be monitored by the number of offspring per female (Vincent et al. 1995) or as the number of fawns per reproducing female (i.e., females with fawns at heel; Boutin et al. 1987). However, for polytocous species such as roe deer, the pattern of variation of reproductive performance as assessed by sampling females can be blurred by differential family effects in relation to cohort quality, since in poor cohorts fawns born in the same family commonly have similar fates (i.e., both die or both survive in most cases), whereas there is no family effect during good years (Gaillard et al. 1998b). Further work is therefore required to assess the suitability of such indicators for management.

The abundance of resources, and the level of their use, can be measured easily on woody plants (Aldous 1944). However, there are strong biases due to differences among observers in their estimations of plant cover (Morellet 1998). The browsing index has, therefore, been developed (Morellet et al. 2001); this is calculated for each plant species using sample plots of 1 m^2 as the proportion of plots in which that species was browsed. Data on the presence/absence of plant species and of signs of browsing on them in quadrants of 1 m^2 have been found to be much more repeatable, and therefore better indices of the abundance and use of resources (Morellet et al. 2001; Morellet et al. 2003).

11.4   Management

For the management of populations of large herbivores to succeed, it needs to be based on (Nichols et al. 1995; Cederlund et al. 1998):

- an assessment of the current state of the animal–habitat relationships based on monitoring ecological changes
- an analysis of the range of possible alternatives to population counts, based on the system's current state, on ecological principles (such as density dependence; see Fig. 11.1), and on the benefits and costs of the possible states to human society
- a choice of management actions by the different stake-holders based on a vision of the optimal future state of the animal-habitat relationships, taking into account uncertainty as to the consequences of management actions in complex systems

Such management is 'adaptive'; its essence is the use of a wide range of indices of animal abundance and condition, and ideally of the abundance of resources and the impact of the animals on resources and on human activities. Managers learn about systems as they manage them (Lancia et al. 1996). Adaptive management (Walters 1986) deals with scientific uncertainty by incorporating a set of models representing the competing hypotheses about system responses to management (Runge and Johnson 2002). With adaptive management the information on the system response to management is gathered continuously so that the information is used to improve biological understanding and to inform future decision-making (Nichols et al. 1995; Shea et al. 1998; Williams et al. 2002). Variations on the theme of adaptive management are used in many wildlife management areas (du Toit 2002).

The two essential decisions in the management of populations of large herbivores concern (1) the objective and (2) the quota. The objective is often decided simply on the basis of the objectives of hunters, but should be based on a wide range of considerations of the benefits and costs of high/low densities of large herbivores for society as a whole (taking into account ethical, social and economic dimensions) as proposed in Cederlund et al. (1998).

Having decided on the objective, which could be to increase the population, decrease it, or maintain the current size, the quota needs to be decided. Given that the approach based on indicators of ecological changes proposed above do not provide information on population sizes, the quota will initially have to be chosen on the basis of expert opinion, and it will be necessary to take into account the size of the target species and its feeding type. The potential population productivity of small and large grazers and browsers are given in Fig. 11.3; intermediate feeders will have intermediate productivities. As expected, it appears that the population productivity is higher for a given relative population size of small than of large species and of browsers than of grazers. Small browsers are thus expected to be much less sensitive to hunting and/or poaching impact than large grazers.

The quota should then be applied for three years or more, without change, in order to get estimates of the ecological indicators for a given hunting pressure, so that the success of the management can be judged from the monitoring. In the initial
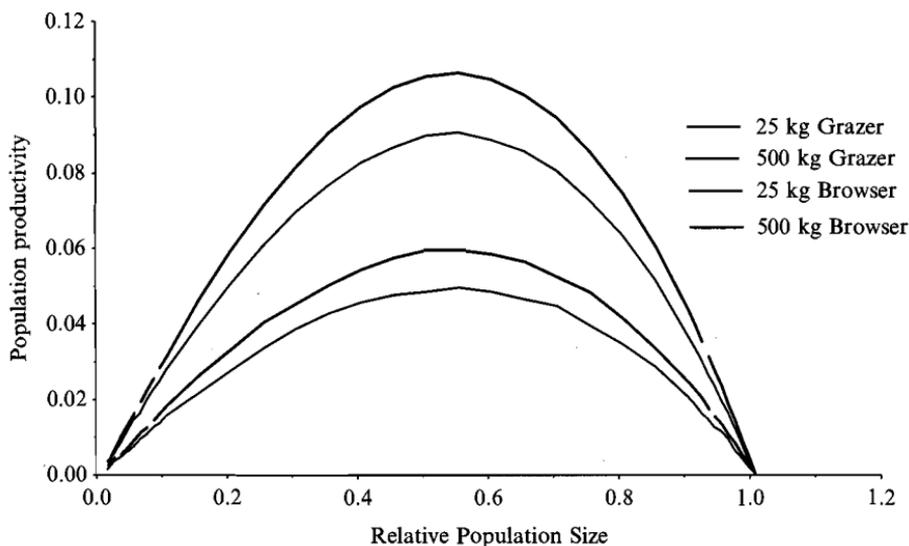
Fig. 11.3 Population productivity (measured as the population increase over two consecutive years) as a function of population size for small (25 kg) and large (500 kg) browser and grazer. To get estimates of population productivities, we used a Leslie demographic model parameterized with the demographic parameters expected for 25 and 500 kg browsers and grazers (as derived from the allometric relationships presented in the text). We thus obtained estimates of population growth (r=0.324 for a 25 kg browser, 0.275 for a 25 kg grazer, 0.275 for a 500 kg browser, and 0.181 for a 500 kg grazer). Then we used the Fowler's equation relating the relative population size at which the maximum sustainable yield occurs in a population (R), its population growth and its generation time (Fowler 1988). We obtained very similar R values among the four case studies (from 0.536 for a large grazer to 0,560 for a small browser). We thus used a constant R of 0.55. We then calculated the population productivity as a function of N, r, and R by using the theta logistic function (Lande et al. 2003)

stages, the management of populations of large herbivores cannot be more accurate than a trial-and-error process dictates, however, as managers gain knowledge of the population–environment system over the years, management will become more finely tuned. Such an approach is thus based on long-term monitoring: the longer the system is monitored, the better it is understood.

11.5 Conclusions

The main source of variation in the life history of large herbivores is the body size of the animal. However, the feeding type, i.e., grazing or browsing, also influences the turnover of the population, being faster for browsers and slower for grazers, but the relatively more important role of adult survival as compared to recruitment parameters on the population growth rate of large herbivores does not change. Feeding type strongly affects the use of habitat and the size of the groups the

animals live in. This means that different methods need to be used for the monitoring and management of grazers and browsers. Management should be adaptive, based on the biology of the animals, and appropriate monitoring of ecological and socio-economic changes in the animal–habitat relationships.

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