

Chapter 6

Population Dynamics of Browsing and Grazing Ungulates in the Anthropocene



Christian Kiffner and Derek E. Lee

6.1 Introduction

Ungulates (here defined as terrestrial artiodactyls and perissodactyls; hoofed animals within an average female body mass of 1–1000 kg) are a highly diverse group of grazing and browsing animals. Despite their cultural, economic, and ecological importance across their nearly worldwide range, the status of many ungulate populations is worrisome (Ripple et al. 2015). Therefore, we address the topic of ungulate population dynamics from the perspective of conservation biology. Our framework is the “declining population paradigm”, which aims at identifying demographic causes and mechanisms that underlie observed changes in population growth rates (Caughley 1994). We mainly focus on ungulate assemblages in temperate zones of Europe and North America, subtropical deciduous forests of South Asia, and savannas and woodlands of Africa, since most relevant research on ungulate population ecology has been carried out in these systems. Due to the high diversity of ungulates in African savannas (Olf et al. 2002), and our own experience, several examples in this Chapter were drawn from this region. Ungulates comprise a huge diversity of species that occur on most continents (Olf et al. 2002), and can functionally be grouped according to their feeding strategy as grazer (eating grass) or browser (eating woody and non-woody dicots) (Hofmann and Stewart 1972). This classification is generally not dichotomous because many species are intermediate (or mixed) feeders (Gagnon and Chew 2000; Codron et al. Chap. 4), and even archetype browsers such as giraffes (*Giraffa camelopardalis*) may occasionally feed

C. Kiffner (✉)

Center for Wildlife Management Studies, The School for Field Studies, Karatu, Tanzania
e-mail: ckiffne@gwdg.de

D. E. Lee

Wild Nature Institute, Concord, NH, USA

Department of Biology, Pennsylvania State University, University Park, PA, USA

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on grasses (Seeber et al. 2012), just as typical grazers may occasionally browse (Owen-Smith 2008). We used this dichotomy even though we are aware that this is an oversimplification (Codron et al. Chap. 4; Gordon and Prins Chap. 16). For analyses, in this Chapter we characterize ungulates as either predominantly grazers ($\geq 50\%$ grass in diet) or browsers ($\geq 50\%$ dicots in diet). With this coarse dichotomy, and its inherent limitations in mind, we will focus on the following specific questions:

1. How does spatial and temporal variability of vegetation productivity affect grazers and browsers?
2. How do densities of grazers and browsers relate to body mass?
3. Which demographic rate contributes most to population growth of browsers and grazers?
4. What are the causal factors of population growth in ungulate populations?
5. Are browsers or grazers more susceptible to anthropogenic changes?

6.2 Spatial and Temporal Variability in Grass and Browse Availability

Forage abundance is the principal driver of second- and third-order habitat selection of animals (i.e., the distribution of home ranges and space utilization within the home range, respectively), and thus largely controls the distribution and density of ungulates (Johnson 1980; Pettorelli et al. 2009; Waltert et al. 2009); although scale-dependent trade-offs between forage quantity and quality exist (Van Beest et al. 2010).

The global distribution of tree cover is mainly affected by climate, but at intermediate precipitation and mild seasonality, fire is the main force differentiating savannas from forests (Langevelde et al. 2003; Staver et al. 2011). Without fire, closed forests could double in their extent (Bond et al. 2004). In arid and semi-arid regions, woody cover is limited by precipitation, fire, and herbivory, which interact to limit woody cover. Competition with grasses also limits recruitment of woody vegetation (de Waal et al. 2011; Morrison et al. 2018). In areas with precipitation exceeding 650 mm, savannas may transform to forests (and vice versa) following perturbations (Sankaran et al. 2005; Murphy and Bowman 2012). The presence or absence of ungulates can also affect vegetation structure and quantity both directly and indirectly. For example, browsing may limit woody species expansion, and thus indirectly stimulate grass growth, which increases fuel load and fire intensity, which further reduces woody cover (Langevelde et al. 2003). Alternatively, high densities of grazers can remove ground fuel to the point where fire prevalence is reduced and woody plant cover increases (Roques et al. 2001). Indeed, fire and herbivory strongly interact. For example during times of culling programs (and thus reduced herbivore densities) the lowered grazing pressure substantially led to increases in the extent of fires whereas the opposite was true during times after the culling

programs when herbivores doubled in biomass density (Smit and Archibald 2019; cf. Smit and Coetsee Chap. 13). Particularly for grazers, these two alternative stable biome states are important because closed-canopy forests have almost no grasses (Ratnam et al. 2011) and reduced productivity in the ground vegetation layer (Melis et al. 2009).

Temporally, browse availability is relatively constant across years, but is influenced by recent precipitation (Rutherford 1984). Browse availability often varies seasonally, as during the dry season in sub-tropical deciduous forests, and during winter in temperate broad-leaved forests, when most of the woody vegetation sheds leaves. Grass availability is more strongly influenced by seasonal and inter-annual differences in rainfall (O'Connor et al. 2001; Ogutu and Owen-Smith 2003). In African savannas, the protein content of both browse and grasses (and thus the nutritional quality) is usually highest during the early rainy season and lowest during the dry season (Pellew 1983; Prins 1988; Robbins 1993).

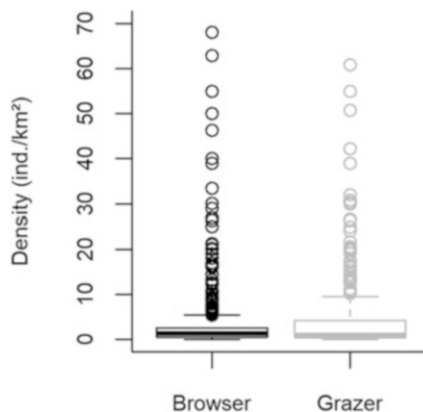
Ungulates have adopted two main strategies to cope with the spatiotemporal variability in food resources. Mixed feeders, such as red deer (*Cervus elaphus*) or impala (*Aepyceros melampus*), can adjust their feeding strategies and mainly feed on grasses during the grass growing season and increase intake of woody vegetation during winter or dry seasons (Meissner et al. 1996; Verheyden-Tixier et al. 2008). Other ungulate species track the spatiotemporal variation in plant phenology by migrating to areas of higher forage quantity and quality (Merkle et al. 2016). Seasonal migrations have been documented for browsers such as roe deer (*Capreolus capreolus*) and moose (*Alces alces*), and grazers such as wildebeest (*Connochaetes taurinus*) and saiga antelope (*Saiga tatarica*), but most of the farthest long-distance migrations are undertaken by grazers (Teitelbaum et al. 2015).

6.3 Population Densities of Grazers and Browsers

To describe patterns and assess correlates of population densities of grazers and browsers, we compiled a database of density estimates of ungulate populations ($n = 964$) across the globe (available at http://www.wildnatureinstitute.org/uploads/5/5/7/7/5577192/kiffner_lee_ungulate_densities.xlsx). We are aware that the broad distinction into grazers and browsers (and even a trichotomy of browsers, mixed feeders, and grazers) is too simplistic from evolutionary and morphological perspectives (Codron et al. Chap. 4). Yet, in order to find broad patterns in population densities, a simplification into two categories (and thus sufficient sample sizes for each “feeding” category) was necessary to allow for our quantitative comparisons.

Population densities of browsers and grazers are highly variable (Fig. 6.1). Although most populations range around a few individuals km^{-2} , both grazing and browsing species can reach very high population densities (with 267 ind. km^{-2} , chital *Axis axis* had the highest density in our dataset; Wegge and Storaas 2009). In

Fig. 6.1 Boxplot showing the range of population density estimates for browsing and grazing ungulates. The highest density in our dataset ($267 \text{ chital.km}^{-2}$) was removed



this and subsequent sections, we outline how this variation in population densities of ungulates can be explained.

Body mass is one of the most fundamental traits of organisms (Peters 1983), and its relationship with population density has received substantial attention from a macro-ecological perspective (Damuth 1981; Blackburn and Gaston 1999; Olf et al. 2002; White et al. 2007). Negative relationships between the \log_{10} body mass and \log_{10} density of animals often have been reported, but the relationships are often non-linear and explain relatively little of the observed variation in animal population densities (Blackburn et al. 1994; Silva et al. 2001). The frequently observed explanation provided for this pattern is that animal abundances are limited by energy availability, but this explanation has been substantially challenged (Blackburn and Gaston 1999; White et al. 2007). To assess whether body mass is a strong predictor of ungulate densities, we plotted trend lines using best fitting (based on sample-size corrected AIC_c scores) general additive models in R (R Core Team 2016; Wood et al. 2016) to non-transformed data.

Our data indicate that relationships between ungulate density and average female body mass are—if at all—rather weak when analysed separately for grazers and browsers, or combined for all ungulates, and that body mass explains very little of the observed variation (Fig. 6.2). Particularly among grazers, biomass density (density \times average female body mass) seems to have a bimodal distribution, with highest biomass densities in species of about 200 kg body mass. Rather than a linear body mass–density relationship, our data indicate that high ungulate densities are realized in specific body mass ranges. Globally, highest population densities (10% of highest densities in our dataset) occur in relatively small-bodied browsers (range: 20–233 kg; median: 45 kg) whereas highest densities in grazers are realized across a wider body mass range and typically in larger species (range: 17–325 kg; median: 137.5 kg). Extending this selection to the 20% highest population densities yielded similar body mass ranges for both browsers (range: 5.5–233 kg, median 45 kg) and grazers (range: 17–325 kg, median 50 kg), lending further support for upper and

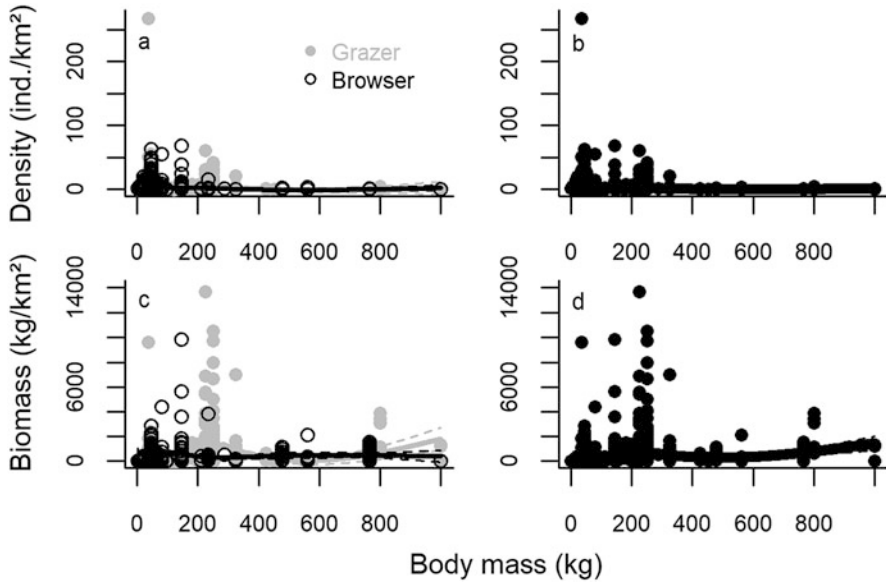


Fig. 6.2 Global patterns of grazer and browser (a) densities and (c) biomass densities in relation to average female body mass as well as the overall relationship between (b) ungulate density and (d) biomass and body mass

lower body size thresholds, beyond which smaller- or larger-sized species cannot obtain densities that are occasionally realized by medium-sized ungulates (Fig. 6.2).

Regional body mass–population density relationships (Fig. 6.3) occasionally support a negative, nonlinear but rather weak trend, particularly among browsers in temperate ecosystems of North America (Fig. 6.3a) and Europe (Fig. 6.3b), and grazers in South Asia (Fig. 6.3c). In African savannas, medium-sized grazers have the highest population densities (Fig. 6.3d)—a pattern found also in savannas of the Tarangire–Manyara ecosystem in northern Tanzania (Fig. 6.3f, g). However, in Miombo woodlands of East Africa, no body mass–population density relationships are apparent (Fig. 6.3e). In temperate zones (North America, Europe), browsers reach higher densities than grazers, whereas in tropical and subtropical regions, grazers tend to reach highest densities. This pattern is even more pronounced in body mass–biomass density relationships. In the northern hemisphere, browsers usually contribute more to overall ungulate biomass (Fig. 6.4a, b), whereas in tropical and subtropical regions, grazers tend to reach higher biomass densities (Fig. 6.4c, g). In South Asia, large-bodied, predominantly grazing gaurs (*Bos gaurus*: 800 kg), contribute substantially to overall ungulate biomass. In African savannas, grazers between ~200–400 kg of body mass contribute most to biomass densities. Although some wild ungulates can reach exceptionally high densities, livestock species frequently surpass densities of wild species in areas where wildlife and livestock coexist (Fig. 6.3h), and their contribution to overall herbivore biomass (Fig. 6.4h)

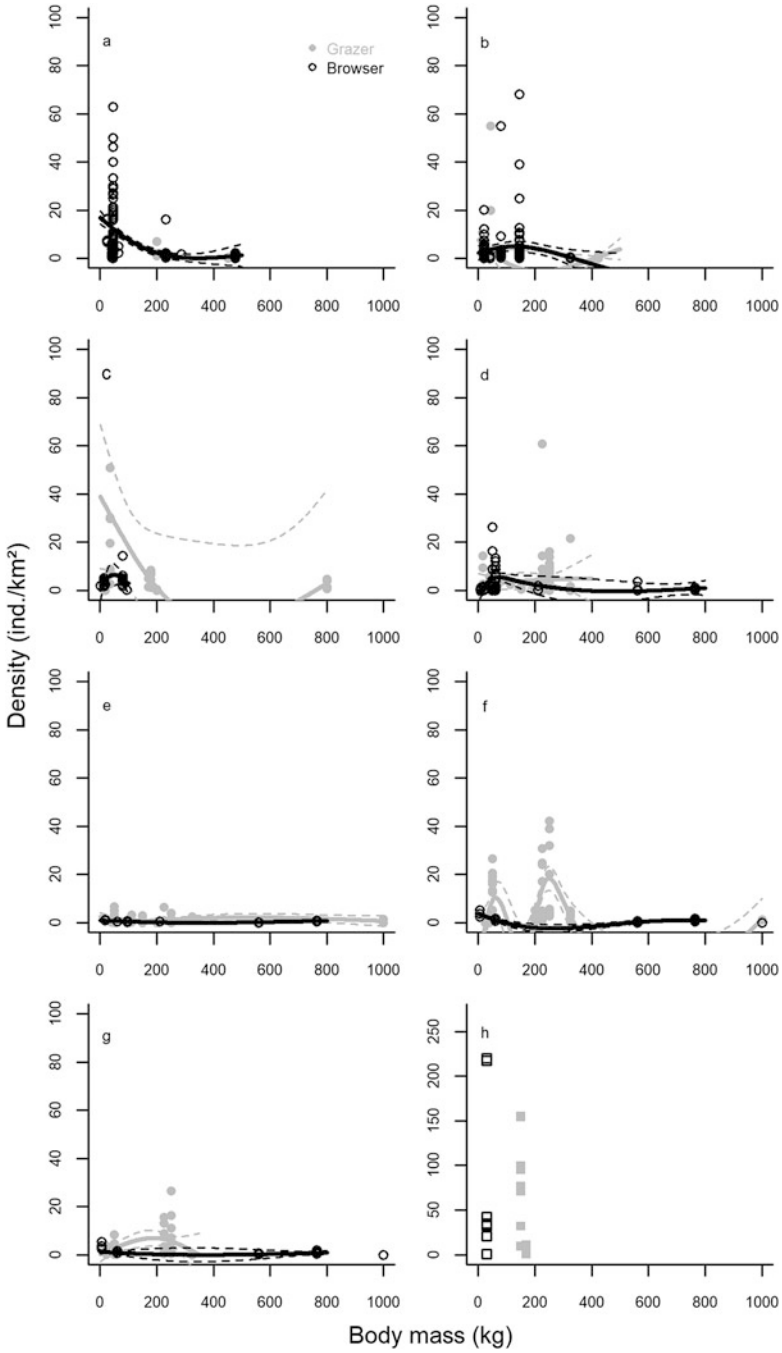


Fig. 6.3 Densities (ind.km⁻²) of grazing and browsing wild ungulates in relation to the average female body mass (kg) in (a) Europe, (b) North America, (c) Southeast Asia, (d) and Africa. For the

usually exceeds those of wild ungulates (Prins 1992; Kiffner et al. 2016; Hempson et al. 2017; Mishra et al. Chap. 7).

These global-, continent-, and ecosystem-wide analyses indicate that the body mass–density relationships are not very strong, and suggest that medium-sized ungulates usually realize the highest densities. A possible explanation for this pattern could be found in the physiological constraints associated with body mass (see also Codron et al. Chap. 4). Small-sized species typically require high forage quality to sustain their proportionally high energy demands, and high-quality forage is usually rare in the environment. At the other body-size extreme, very large herbivores usually require proportionally greater amounts of forage (Müller et al. 2013). These considerations imply that small ungulates are mainly constrained by availability of high-quality forage; very large ungulates are mainly constrained by forage quantity in the environment; whereas medium-sized ungulates are less severely constrained by forage quality and quantity. These physiological considerations may partly explain observed patterns of highly abundant medium-sized ungulates, and low abundances of very small and very large ungulates.

Beyond among-species density differences, within-species variation in densities can be substantial. Indeed, within-species coefficients of variation ($CV = \text{standard deviation of density estimates} / \text{mean density}$) were clustered between 0 and 2 (Fig. 6.5). CVs in both grazers and browsers were not significantly correlated with sample size (grazer: $\tau = 0.12$, $p = 0.37$, $n = 27$; browser: $\tau = 0.30$, $p = 0.07$, $n = 20$). In grazers, variability in density is generally negatively correlated with body mass, and above a body mass of ~ 100 kg tends to be lower than for browsers (Fig. 6.5a). In browsers, the body mass–coefficient of variation relationship is hump shaped with highest variability in densities among browsing species of 200–600 kg body mass. Among grazers, our dataset indicates particular high variability in densities of fallow deer (*Dama dama*), chital, southern reedbuck (*Redunca arundinum*), and African buffalo (*Syncerus caffer*). Browsers with highly variable densities were red deer, wild boar (*Sus scrofa*), bushbuck (*Tragelaphus scriptus*), and eland (*Taurotragus oryx*). Across all ungulates, we found variability in densities was negatively associated with body mass (Fig. 6.5b). In the following sections, we will outline how abiotic and biotic factors cause variation in demographic processes leading to variation in population growth.



Fig. 6.3 (continued) African continent, wild ungulate densities are presented separately for (e) Miombo ecosystems, (f) national parks and (g) community-based conservation areas in the Tarangire-Manyara ecosystem (Tanzania). (h) Depicts densities of livestock species (note the different y-axis scale) in community-based conservation projects of the Tarangire-Manyara ecosystem (Tanzania)

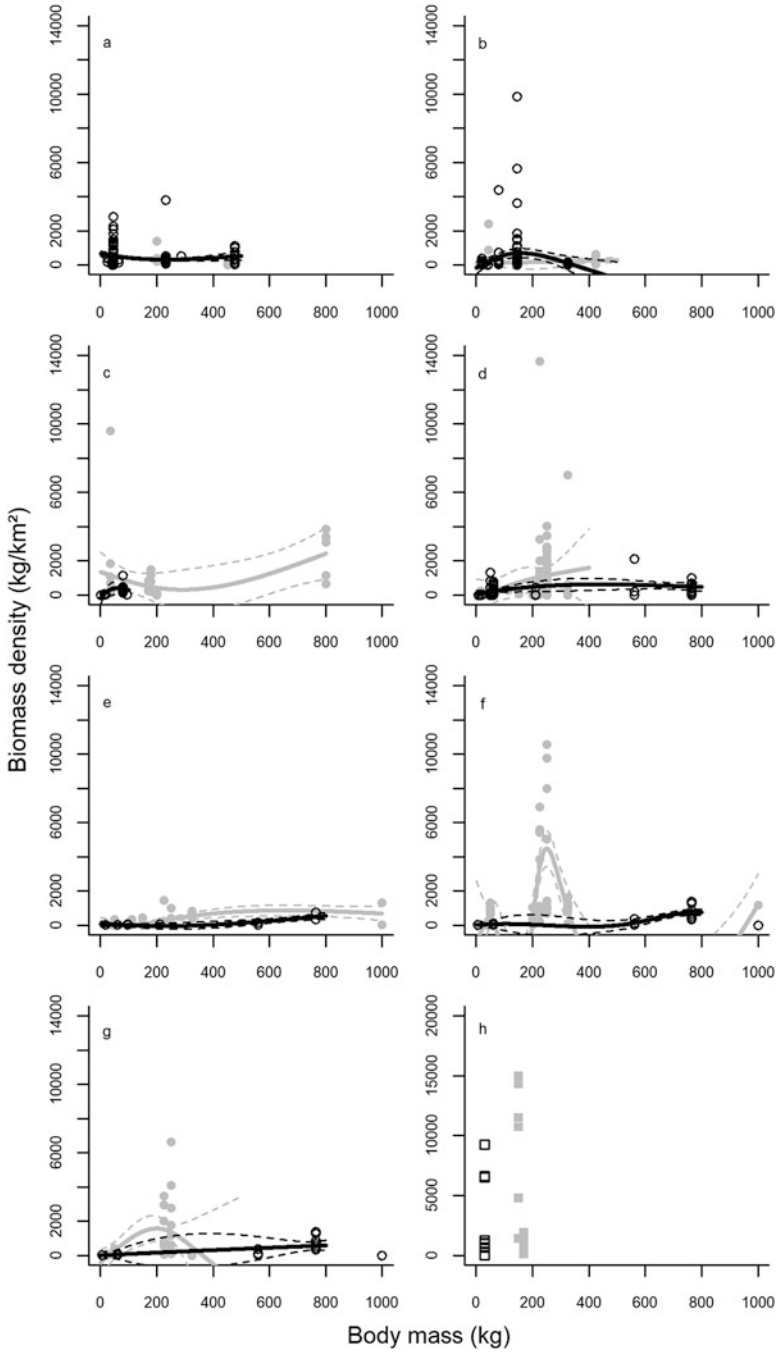
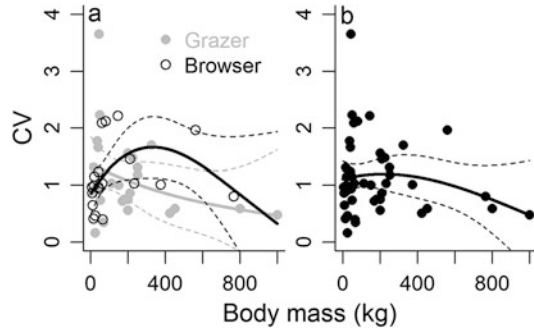


Fig. 6.4 Biomass densities (kg.km⁻²) of grazing and browsing wild ungulates in relation to the average female body mass (kg) in (a) Europe, (b) North America, (c) Southeast Asia, (d) and

Fig. 6.5 Coefficient of variation (CV; 1 = 100%) of population densities (a) in grazing and browsing ungulates and (b) all grazers and browsers combined in relation to body mass. We only computed CVs for species with ≥ 3 density estimates



6.4 Demographic Patterns and Processes Underlying Population Dynamics

The numbers of individuals in animal populations fluctuate over time and across space (Lack 1966; Levins 1969; Sinclair 1977). Changes in population sizes are ultimately due to the demographic processes of births, deaths, and movements (immigration and emigration). Identifying which specific demographic rate (birth rate, juvenile survival, adult survival, age of first reproduction, immigration, or emigration) contributes most to changes in population growth (i.e., the “key demographic rate”) can be considered the “holy grail” of population ecology (Gaillard et al. 1998, 2000; Morris and Doak 2002; Coulson et al. 2005), and is of great interest to studies of life history evolution and conservation biology. Our current synthesis of population ecology studies suggests that no specific demographic rate is central in governing all or most changes in growth rates, and that environmental variation in resource availability and predation directly and indirectly affect vital rates. In addition, indirect effects of perturbations can create cohort effects or alter age structures. This leads to transient population dynamics because different cohorts and age classes have different demographic rates. The relative contribution of direct vs. indirect effects can be dependent upon the life history strategy (slow versus fast) of the species (Gamelon et al. 2016). This suggests that all age groups contribute to changes in population growth (Gamelon et al. 2016). Furthermore, there is increasing evidence that ungulates can flexibly adjust reproductive tactics (and thus influence population growth) in response to environmental variation such as pulsed increases in food quantity and quality (Gamelon et al. 2017). This understanding



Fig. 6.4 (continued) Africa. For the African continent, wild ungulate biomass in (e) Miombo ecosystems, (f) national parks and (g) community-based conservation projects in the Tarangire-Manyara ecosystem (Tanzania) are presented as well. (h) Depicts biomass densities of livestock species (note the different y-axis scale) in community-based conservation projects of the Tarangire-Manyara ecosystem (Tanzania)

of ungulate population ecology has developed over time, which we will now briefly summarize.

Early syntheses of empirical studies of ungulate population dynamics examined temporal variation in demographic rates in relation to population growth rates (Gaillard et al. 1998, 2000). Their main findings were that adult female survival showed low inter-annual variation, fecundity of prime-aged females was moderately variable, and juvenile survival and young female fecundity showed the greatest inter-annual variation. Interestingly, although matrix population models indicated adult survival theoretically makes the greatest contribution to population growth, it had very low observed inter-annual variability, leaving little room for adult survival to have an appreciable effect on population growth. Conversely, juvenile survival theoretically had a low contribution to population growth rate, but exhibited large temporal variation that was primarily responsible for observed changes in population size, and thus was identified as the key demographic rate (Wisdom et al. 2000; Lehman et al. 2018).

Albon et al. (2000) sought the key demographic rate for red deer on Isle of Rum, Scotland and made a slightly more nuanced conclusion, finding that birth rate was the dominant component of relative population growth rate when the population was growing rapidly, but during a period when population size fluctuated near carrying capacity, variation in adult female survival (along with covariation of adult survival and calf survival) contributed most to relative variation in population growth rate. Clutton-Brock and Coulson (2002) also found that variation in the survival of mature animals contributed more to changes in population size than juvenile survival. Subsequent work (Coulson et al. 2005) indicated that the most influential demographic rates varied among populations of red deer and bighorn sheep (*Ovis canadensis*) depending on whether the population was growing or fluctuating near carrying capacity, and according to site-specific differences in ecological processes such as disease, predation, and density dependence. Recent studies have found that in declining populations, variation in adult survival, due to natural or anthropogenic predation, can be the most important factor affecting variation in population growth rates (Johnson et al. 2010; Lee et al. 2016a). Importantly, covariation among demographic rates within a population is a critical feature that should be considered when seeking the demographic causes of variation in population growth rate (Coulson et al. 2005).

Environmental variation among years such as temperature- or precipitation-dependent timing of plant phenology relative to timing of birth can affect all the newborns in an area similarly, creating cohort effects (Clutton-Brock and Coulson 2002). In years when food is scarce for all pregnant females in an area, offspring birth weights can be low and bodily growth of juveniles can be slower, and this can lead to lower demographic rates throughout the lives of all individuals born in a “bad” year cohort (Post and Stenseth 1999). Indeed, up to 50% of variation in individual performance within a population can be explained by early life environment in ungulates (Hamel et al. 2009).

Stochastic variation in population age structure (the distribution of different-aged animals in a population) is important because different ages have different

demographic rates. Environmental variation can alter the age-structure distribution which causes transient population dynamics that are mediated by life history (Owen-Smith and Mason 2005; Haridas et al. 2009; Coulson et al. 2010). Fast-paced species (with a short generation time) usually increase population growth rates after disturbance, whereas slow-paced species (with a long generation time) frequently decrease growth rates after disturbance (Gamelon et al. 2014).

The demographic mechanisms underlying observed population dynamics are clearly complex, and suggest strong context dependencies (Clutton-Brock and Coulson 2002). Conservation and species recovery programs are most effective when system-specific contributions of demographic rates to population growth rates are known. In identifying demographic rates driving the dynamics of populations, analyses should incorporate transient dynamics, and actual variation in demographic rates. This requires data on demographic rate means, variances and covariances, and population sizes divided into age or stage distributions (Johnson et al. 2010). Integrated population models (Kery and Schaub 2012) and transient life table response experiments (Koons et al. 2016, 2017) that incorporate environmental stochasticity (Tuljapurkar 1982), correlations among demographic rates (Coulson et al. 2005), and non-stationarity (Jenouvrier et al. 2014) are useful tools for analysing demographic mechanisms underlying population fluctuations (Maldonado-Chaparro et al. 2018).

Metapopulation analyses are rarely conducted for large herbivores (Lee and Bolger 2017), but the theory of metapopulation dynamics that has arisen from studies of other species should be tested for applicability to grazers and browsers. Particularly important from a conservation perspective in increasingly anthropogenically fragmented habitats, is the idea that metapopulations can buffer subpopulation oscillations and reduce subpopulation extinction probabilities (Goodman 1987; Gilpin and Hanski 1991; Hess 1996).

6.5 Global and Local Causal Factors Underlying Ungulate Population Dynamics

In recent years, ecologists have moved away from mono-causal hypotheses explaining animal population dynamics, and developed more complex models, which propose that primary production, predation, droughts, fire, and land conversion (and possible other factors) all interact synergistically in their regulation of herbivore populations to create indirect-, additive-, reciprocal-, and interaction-modifying relationships (Hopcraft et al. 2010). There is increasing quantitative evidence that abiotic factors determine the relative importance of predation, forage quantity, and forage quality in regulating herbivores of different body sizes, and this alters the relative strength of the connections between biotic and abiotic components in ecosystems. Species with smaller body masses are often subject to greater levels of top-down control (mainly owing to their susceptibility to a more diverse set of predators), whereas body mass thresholds for escaping predation regulation, appear

context dependent (Hopcraft et al. 2010). In sum, larger-sized species are mainly limited by food supply whereas the effect of predation may be most influential in relatively small species (Hopcraft et al. 2010), and in less productive environments (Melis et al. 2009).

At the core, theory of ungulate population dynamics needs to explicitly incorporate temporal and spatial aspects of environmental variation (Boyce et al. 2006; Hempson et al. 2015). Forage availability determines individual body condition and, therefore, survival and reproduction in ungulates (Parker et al. 2009), so resource availability (“bottom up regulation”) is the ultimate causal factor determining population size and trajectory (Sinclair and Krebs 2002; Sinclair 2003; Pettorelli et al. 2009). Indeed, the observed variation in population densities of herbivores is primarily driven by primary production, which itself is mainly governed by soil fertility and precipitation. Thus, primary productivity is the main determinant of maximum density for a population (Coe et al. 1976; East 1984; Fritz and Duncan 1994; Pettorelli et al. 2009).

Internal feedbacks of population density (i.e., density dependence) may affect population growth of large ungulates to some degree as well (Bonenfant et al. 2009). High population density, that approaches or exceeds local carrying capacity, generally results in body mass decreases, increases in age of first breeding, and decreases in all aspects of reproduction from ovule production to weaning success, thereby generally reducing recruitment (Bonenfant et al. 2009). Survival during the first year is the demographic rate most frequently reported to be density dependent, and it also shows the greatest variation with density, but prime-aged adult survival and costs of reproduction are also density dependent (Bonenfant et al. 2009). Dispersal may also be affected by density (Matthysen 2005). There is substantial evidence that the relative importance of density dependence for regulating large herbivore populations is itself dependent on spatiotemporal variation in resources and predation. Temporal environmental variability has been associated with density dependence caused by forage deficits (Wang et al. 2006), and—among ungulates in the northern hemisphere—predation and spatial resource heterogeneity may weaken the density-dependent effects (Wang et al. 2009). At least some larger ungulate species may flexibly adjust their reproductive allocation in response to resource availability, such as pulsed resource availability caused by mast seeding (Gamelon et al. 2017). These examples show that spatiotemporal variation in resource availability and predation interact with density dependence and reinforce the notion that resource availability is the ultimate factor affecting population growth and density of ungulates.

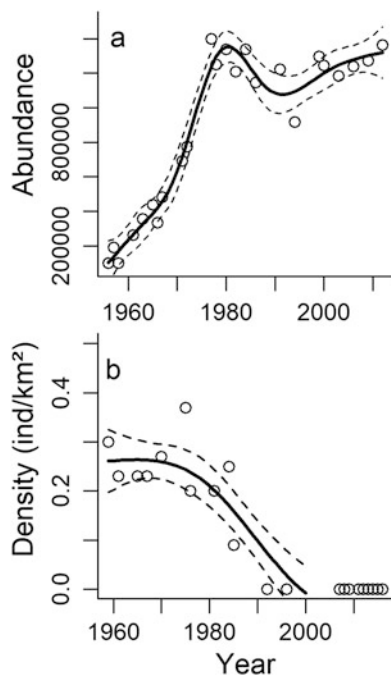
The concept of the key resource for ungulate populations is defined as that resource which determines the demographic rate that exerts the most influence on the population trajectory (Illius and O’Connor 1999). Thus identifying the key resource for a population is useful for determining the specific pathway to population regulation. Resource availability often varies over time and annual variation in primary productivity is largely determined by atmospheric oscillations (El Niño Southern and North Atlantic Oscillations) affecting precipitation and temperature patterns, with direct impacts on vegetation phenology and primary productivity and,

therefore, populations of ungulates (Post and Stenseth 1999; Ogotu et al. 2008; Hagen et al. 2017). Theoretically, spatial heterogeneity can buffer populations against temporal variability by allowing herbivores to access forage resources in the most nutritious state (Wang et al. 2006; Hobbs and Gordon 2010), via dispersal before forage is depleted (Owen-Smith 2004). However, localized weather extremes (e.g., reduced dry season rainfall), and increasingly restricted animal movement caused by fencing or other forms of habitat fragmentation, may amplify negative effects of large-scale climatic variation on ungulate populations (Ogotu and Owen-Smith 2003).

Stochastic disturbances, such as natural- and human-induced variation in climate extremes (droughts, cold, flooding), can directly (via increased mortality) and indirectly (via changes in available food resources) affect ungulate population growth rates. Sudden shifts in local primary productivity, due to perturbations such as fire, flood, or land conversion, can rearrange the dynamics of an ecosystem briefly or semi-permanently into a new state (van de Koppel et al. 2002). In temperate latitudes, harsh winters can strongly affect mortality rates, particularly among younger age classes, through a combination of greater thermoregulatory costs and decreased forage availability because of deep snow (Post and Stenseth 1999; Jacobson et al. 2004). In tropical or subtropical systems, droughts can directly affect mortality rates (Owen-Smith 1990), with more sedentary, grazing, and mixed-feeding species at highest risk from increasing drought intensity (Duncan et al. 2012). Human-caused increases in the atmospheric CO₂ concentration can act as fertilizer for plants in general, but woody vegetation appears to benefit most from CO₂ enrichment (Bond and Midgley 2000). Changes in herbivory, precipitation, and fire frequency may also affect woody versus herb–grass plant community composition locally (Morrison et al. 2016a), but CO₂ is considered to be the key underlying causal factor of shrub encroachment in savanna ecosystems (Devine et al. 2017).

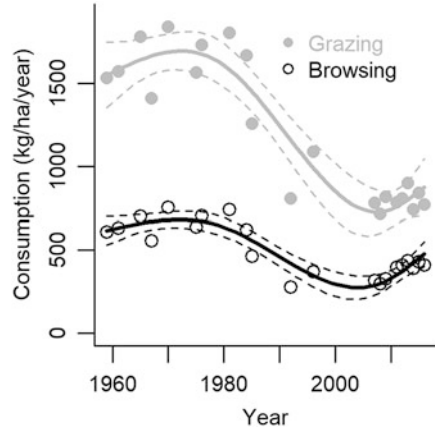
Predation and diseases (“top down regulation”) can reduce populations below their resource-determined potential carrying capacity. A famous example of top-down regulation is the six-fold increase in the Serengeti wildebeest population (Fig. 6.6a) after the population was released from the rinderpest virus (Sinclair 1979; Holdo et al. 2009). A more pessimistic example is the trajectory of the black rhinoceros (*Diceros bicornis*) population in Lake Manyara National Park, Tanzania (Fig. 6.6b) that was extirpated within few years due to poaching (Kiffner et al. 2017). Albeit classic top-down theory involves direct (mortality) effects, there is growing evidence that the mere presence of predators can affect demography and reproduction of ungulate species through behavioural and physiological effects of fear (Creel et al. 2007; LaManna and Martin 2016), but non-lethal effects of predation have yet to be fully integrated into models of population regulation (Peers et al. 2018). Although population growth is usually negatively correlated with population density, population growth rate and density can be positively associated at low abundances (Courchamp et al. 1999). This phenomenon (often named *Allee effect*) can be caused by predation or reduced reproduction, and can lead to increased local extinction risk of ungulates that occur at low densities (Wittmer et al. 2005; Bourbeau-Lemieux et al. 2011).

Fig. 6.6 Time series of wildebeest (*Connochaetus taurinus*) population sizes in the Serengeti ecosystem (data from Hopcraft et al. 2015) and densities of black rhinoceros (*Diceros bicornis*) in Lake Manyara National Park (data from Kiffner et al. 2017)



In most ecosystems, multiple ungulate species co-exist, which may cause competition over commonly used food resources. Indeed, correlative studies suggest that grazing ungulates in East Africa can be limited by competition with buffalo (de Boer and Prins 1990; Kiffner et al. 2017). In Europe, high red deer densities have a negative effect on body masses of roe deer fawns (Richard et al. 2010), and time series of herbivore assemblages suggest that interspecific competition affects ungulate population dynamics in temperate forests (Jędrzejewska et al. 1997). Facilitation within herbivore assemblages has been documented in tropical and subtropical ungulate communities as an important process governing coexistence (Olf et al. 2002). While competition over resources usually occurs during times of resource scarcity (when vegetation is dormant), facilitation mainly occurs during the growing season when species such as zebras (*Equus quagga*) stimulate grass growth (Sinclair and Norton-Griffiths 1982; Arsenault and Owen-Smith 2002; Wegge et al. 2006). The relative importance of competition versus facilitation is particularly relevant in areas where livestock species coexist with wildlife (Spear and Chown 2009). Exclusion experiments in Kenya's Laikipia landscape suggest that facilitation mainly occurs during the growing (wet) season, whereas wildlife and livestock compete for grasses during the dry season (Odadi et al. 2011a, b). Indirect effects, such as apparent competition and apparent mutualism among species, mediated by a shared predator, are also possible (Estes et al. 2013), but rarely quantified (Chaneton

Fig. 6.7 Time series of estimated grass and browse consumption ($\text{kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$) as a function of population fluctuations of thirteen herbivore species and estimated daily grass and browse intake in Lake Manyara National Park, Tanzania (data from Kiffner et al. 2017)



and Bonsall 2000; Lee et al. 2016b). Beyond competition and facilitation, evidence from temperate and tropical biomes indicates that wild and domestic ungulates can have substantial cascading effects on plant regeneration, structure, and functioning (Goheen et al. 2018; Ramirez et al. 2018). In turn, this can shape the relative contribution of grazing and browsing (Fig. 6.7), as well as ecosystem structure and functioning (Dirzo et al. 2014; Hempson et al. 2017).

Advanced models to adequately depict ungulate population dynamics, therefore, need to (1) include biotic interactions (which could be additive, reciprocal, indirect, and interaction modifying) between resource availability, competition and facilitation, diseases, and predation; (2) incorporate spatiotemporal variation in abiotic factors, which determine resource availability, the relative strength of competition and facilitation, predation, and diseases in regulating herbivores of different body sizes; and (3) explicitly address possible feedback loops between abiotic factors, biotic interactions, and ungulate populations.

6.6 Predicted Effects of Anthropogenic Perturbations

Developing such models will be particularly important to assess the viability of ungulate populations in increasingly human-dominated landscapes. The most influential anthropogenic perturbations that affect ungulate populations are likely to be (1) land use change; (2) climate change; (3) invasive species (e.g., livestock); (4) increase in atmospheric CO_2 ; and (5) direct, unsustainable exploitation (Sala et al. 2000; Ripple et al. 2015). Some of these upheavals act on global scales (CO_2 enrichment, climate change), whereas others occur more localized (land-use change, invasive species, and direct exploitation). Considering these multiple upheavals, the large diversity of ungulates, strong context dependence, and lack of long time series for most ungulate populations, we used qualitative threat assessment methodology

(Burgman et al. 1993) to provide a general indication of the level of threat for grazers and browsers in temperate and tropical and sub-tropical biomes (Table 6.1). Given the difficulties in predicting indirect effects, we mainly focused on likely direct effects on ungulate populations.

We excluded climate change from the table because direct and indirect climate effects on distribution ranges and physiology of ungulates are likely to be case specific (Bellard et al. 2012; see also **Boone** Chap. 8). For example, in temperate zones and the arctic, milder winters are projected to reduce winter mortality (Loison et al. 1999; Post and Stenseth 1999), for both grazers and browsers. However, altered thawing and refreezing of surface snow in the arctic may substantially affect ungulate movement and possibly mortality (Bartsch et al. 2010). In general, climate change may particularly affect grazers, since variation in climatic conditions will lead to variable grass growth (Ogutu et al. 2008).

Despite the coarse nature of our assessment, Table 6.1 provides a narrative that suggests grazing ungulates are likely to be more negatively affected by human activities compared to browsers—a conclusion that is in line with the prediction that most biodiversity changes will occur in grassland biomes (Sala et al. 2000; Smit and Prins 2015; **Mishra et al.** Chap. 7). Moreover, current mainstream conservation efforts, such as REDD+, focus mainly on woodland conservation or afforestation (Collins et al. 2011), and globally elevated CO₂ concentrations favour woody vegetation to a greater extent than grasses (Devine et al. 2017). Yet, several species which we broadly classified as “grazers” are indeed mixed feeders, and may thus cope relatively well if grasslands transform to woodlands or shrublands as exemplified by sustained and even increasing densities of impalas in changing environments (Kiffner et al. 2016, 2017). However, obligate grazers typically require unrestricted access to large areas of grasslands (Fryxell et al. 2005)—a scenario that is scarce in a world of sustained human population growth (Gerland et al. 2014)—and may thus be particularly impacted by structural landscape alterations such as shrub encroachment, and agricultural and settlement expansions.

Environmental and anthropogenic perturbations rarely act independently from each other on ungulate populations (Dirzo et al. 2014). Indeed, negative effects of single perturbations may be amplified by changes in additional environmental conditions. For example, die-offs of saiga antelope due to bacterial infections were likely facilitated by temperature and humidity anomalies (Kock et al. 2018). Similarly, ungulates in continuous landscapes may be able to cope with seasonal or climate-induced shifts in plant phenology (Cleland et al. 2007), but populations in fragmented landscapes may be substantially affected (Jackson and Sax 2010; Morrison et al. 2016b). Importantly, the human-caused loss of large herbivorous mammals is not only a symptom of the Anthropocene but is now a major causal factor of ecological change (Dirzo et al. 2014). For instance, replacing large, wild ungulates with livestock can reduce fire frequencies, which usually increases woody cover (Hempson et al. 2017). Similarly, loss of mega-herbivores may release woody vegetation from strong herbivore pressure, which may, in return, have cascading effects on vegetation structure, other animal taxa, ecosystem functioning, and ecosystem services (Dirzo et al. 2014; cf. **Sabo** Chap. 11; **Katona and Coetsee** Chap. 12).

Table 6.1 Hypothesized effects of specific anthropogenic perturbations (+ positive effect on populations; - negative effect on populations; 0 no strong effect) on population growth of browsing and grazing ungulate populations in temperate (-Temp) and tropical and subtropical (-Trop) regions

	Land use change	Invasive (livestock) species	CO ₂	Direct exploitation
Browser-Trop	<p>+: Rewilding, i.e., abandonment of agricultural areas increases habitat area (Perreira and Navaro 2015)</p> <p>0: Relative stable forest cover in many parts (Hansen et al. 2013)</p> <p>-: Loss of boreal forests (Hansen et al. 2013)</p>	<p>0: Unlikely to be of high relevance due to little overlap in food resources and husbandry practices in most temperate regions</p>	<p>+: Dicots likely to show increased growth due to CO₂ enrichment in the atmosphere (Norby et al. 2005)</p>	<p>0: Predominately sustainably managed hunting in North America and Europe (Milner et al. 2006)</p> <p>-: Several ungulate species threatened by harvesting in North Asia (Milner et al. 2006)</p>
Browser-Trop	<p>-: Deforestation highest in tropics and subtropics (Hansen et al. 2013)</p> <p>0: REDD+ projects may partially buffer against deforestation (Collins et al. 2011)</p>	<p>0: Unlikely to be of high relevance due to little overlap in food resources</p>	<p>+: Dicots likely to show increased growth due to CO₂ enrichment in the atmosphere (Norby et al. 2005)</p>	<p>-: Large species most vulnerable, mainly due to bushmeat hunting (Wilkie et al. 2011; Ripple et al. 2017)</p>
Grazer-Trop	<p>+: Targeted conservation and reintroduction projects for mega grazers in place (e.g., Kuemmerle et al. 2011)</p> <p>-: Range contraction of grasslands in North Asia (Olson et al. 2011; Buuweiabaatar et al. 2016)</p>	<p>0: Unlikely to be of high relevance due to husbandry practices in most temperate regions</p>	<p>-: Potential for shrub encroachment due to CO₂ enrichment in the atmosphere (Devine et al. 2017)</p>	<p>0: Predominately sustainably managed hunting in North America and Europe and several large grazers strictly protected (Milner et al. 2006)</p> <p>-: Several ungulate species threatened by harvesting in North Asia (Milner et al. 2006; Olson et al. 2014)</p>
Grazer-Trop	<p>-: Conversion to agricultural lands highest in grassland biomes (Sala et al. 2000)</p> <p>-: Fragmentation of migratory ranges (Bolger et al. 2008)</p> <p>0: Annual range of only few populations entirely protected (Hopcraft et al. 2015)</p>	<p>-: Possibility for apparent competition with grazing livestock, particularly in areas with high stocking rates of cattle during the dry season (Odadi et al. 2011a, b)</p>	<p>-: Evidence for shrub encroachment due to CO₂ enrichment in the atmosphere (Devine et al. 2017)</p>	<p>-: Large species most vulnerable, mainly due to bushmeat hunting (Lindsey et al. 2013; Ripple et al. 2017)</p>

6.7 Conclusions

The status of many large herbivores is a cause for concern (Ripple et al. 2015), and our qualitative analysis indicates that grazing ungulate species may be particularly threatened due to multiple anthropogenic perturbations hypothesized to negatively affect their populations (Prins and Gordon 2008; Gordon and Prins 2008). On a more optimistic note, there is ample evidence that large herbivores can thrive outside fully protected areas (e.g., Kiffner et al. 2016; Lee 2018), and that integrating livestock with wildlife can be beneficial for the environment and human well-being (Gordon 2018; Keesing et al. 2018). As a case in point, roe deer and wild boar populations in central Europe, and deer (*Odocoileus* spp.) in North America seem extraordinarily resilient and thrive in human-dominated landscapes to the point that they are considered “overabundant” (Côté et al. 2004; Burbaitė and Csányi 2009; Massei et al. 2015). Although there are some generalities how animals adjust their behaviour in human-dominated landscapes, such as shifting activity to nighttimes (Gaynor et al. 2018) and reducing movement (Tucker et al. 2018), there is a lack of quantitative, integrated, and systematic analyses that investigate how ungulates respond to anthropogenic change with respect to phenology, space use, and physiology (Bolger et al. 2008; Bellard et al. 2012), and how these responses affect population growth. A first (but rarely implemented) step in this direction would be systematic and ecosystem-wide population monitoring to describe the often substantial spatial and temporal variation of ungulate densities. Ideally, such monitoring would be coupled with large-scale metapopulation studies that allow estimation of site-specific demographic rates, to link variation in population growth rates with demographic processes and environmental and anthropogenic perturbations. Such process-oriented understanding is needed to guide effective conservation measures (including restoration attempts) of ungulates and ecosystems (Sinclair et al. 2018).

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