Chapter 4
Grazing and Browsing by Large Herbivores in South and Southeast Asia

Farshid S. Ahrestani, Ignas M.A. Heitkönig, Hisashi Matsubayashi and Herbert H.T. Prins

Abstract Understanding a species' foraging habits and preferences is fundamental to understanding its overall ecology and essential for its management and conservation. In general, large herbivores are classified as either grazers, browsers, or mixed feeders, and a species' diet preference is related to its body mass and digestive trait syndrome. Here, we analyze feeding strategies of large herbivores in South and Southeast Asia (SSEA) as related to their body mass and digestive trait syndromes. Overall, our results are similar to patterns observed on other continents. The majority of large herbivore species in SSEA are mixed feeders. Browsers and frugivores dominate the smallest body mass classes, while bulk feeders, predominantly grazers, dominate the largest body mass classes. There is an absence of hindgut fermenters in the lower body mass classes, and an absence of ruminants in the megaherbivore class (>1000 kg). Cervids in SSEA do not get as large as Bovids, and in both Cervids and Bovids the greatest number of species are found in the smaller body mass classes. Although large herbivores in SSEA occur across a wide range of different habitat types, there are discernible habitat associations with different groups of species. While this chapter sheds light on this important facet of large herbivore ecology in the region, there remains an acute lack of data on the foraging ecology of the majority of species in SSEA.

F.S. Ahrestani (✉)
Department of Ecology, Evolution and Environmental Biology,
Columbia University, New York, NY 10027, USA
e-mail: farshid.ahrestani@gmail.com

I.M.A. Heitkönig · H.H.T. Prins
Resource Ecology Group, Wageningen University,
6708 PB Wageningen, The Netherlands
e-mail: ignas.heitkonig@wur.nl

H.H.T. Prins
e-mail: herbert.prins@wur.nl

H. Matsubayashi
Department of Forest Science, Tokyo University of Agriculture, Setagaya, Japan
e-mail: matsubayashi.hisashi@gmail.com

4.1   Introduction

Understanding a species' food requirements and resource acquisition strategies is fundamental to understanding its ecology. Based on their preference for the two major plant types, monocots (grasses and sedges) and dicots (forbs, shrubs, and trees), large herbivores have historically been classified as either (a) grazers (i.e., bulk and roughage feeders), (b) browsers (selectors of concentrated dicotyledonous herbage), or (c) intermediate or mixed feeders that consume either grass or browse at different seasons or in different areas (Hofmann and Stewart 1972; Hofmann 1973, 1989; Duncan and Poppi 2008). Grass and browse represent very different food resources and their consumption poses different constraints for herbivores (Duncan and Poppi 2008). Browse species, when compared to grasses, have higher levels of soluble cell content and nitrogen that are beneficial for large herbivores, but at the same time have higher levels of lignin and secondary metabolites that are detrimental to large herbivores (Demment and Van Soest 1985; Gordon and Illius 1994; Gordon 2003; Duncan and Poppi 2008). These fundamental differences between grasses and browse have led to different adaptations in animals specializing on one or the other plant type, with implications for all aspects of their ecology and life history (Hofmann and Stewart 1972; Hofmann 1973, 1989; Gordon 2003; Duncan and Poppi 2008).

Based on differences found in the relationships between stomach structure and feeding habits of East African ruminants, Hofmann et al. proposed that a species' digestive trait syndrome was the primary factor deciding forage selection and feeding habits of large herbivores (Hofmann and Stewart 1972; Hofmann 1973, 1989). However, subsequent analyses that statistically accounted for differences in body mass among species found limited evidence for morphological and anatomical differences between large herbivores belonging to different feeding categories (Gordon and Illius 1994; Gordon 2003). Thus, while additional studies have found evidence to support Hofmann's proposition (Clauss et al. 2003, 2008, 2010; Hofmann et al. 2008), it is now widely accepted that body mass plays a critical role in the resource ecology of large herbivores (Prins and Olff 1998).

Hofmann and Stewart (1972) originally proposed their foraging categories based on differences between only ruminant species, which was not surprising considering that 92 % of the ∼260 large herbivore species worldwide are ruminants. All ruminants belong to the order Artiodactyla (even-toed ungulates) and the remaining 8 % of large herbivores are hindgut fermenters that are confined to the mammalian orders Perissodactyla (odd-toed ungulates) and Proboscidea (elephants). Ruminants are foregut fermenters, i.e., they derive the bulk of their energy from the forage they consume before passage through the gut, primarily by the action of symbiotic

microbes on plant material during a fermentation process in the rumen, or a similar morphological structure as in hippos or camelids (Van Soest 1994). In hindgut fermentation, though energy is first derived when food passes through the stomach, additional energy is derived from fermentation of food in the hindgut, primarily the caecum.

The dominance of the large herbivore guild by ruminants is the result of a ruminant radiation that began ~ 10 Ma during the Miocene, which coincided with the expansion and diversification of grasslands worldwide (Perez-Barberia et al. 2001; Prins and Gordon 2008; Bouchenak-Khelladi et al. 2009). The first large herbivores date back to the early Cenozoic (~ 55 Ma), a time when grasslands were not common, which suggests that browsing was the more primitive of the two major large herbivore diets (Bodmer and Ward 2006). However, when grasslands began expanding across the globe around 10 Ma, especially in the tropics, the first specialized grazers—which were primarily ruminants—emerged (Cerling et al. 1993, 1997; Bouchenak-Khelladi et al. 2009). An increasing speciation of ruminants continued to match the expansion of grasslands worldwide, which in turn was being fuelled by the emergence of an alternate to the prevailing C_3 photosynthetic pathway in plants—the C_4 photosynthetic pathway, which enabled plants to function at lower CO_2 levels (Janis 2008; Damuth and Janis 2011).

Although ruminants dominate the large herbivore guild and many ruminants are grazers, the majority of the smallest ruminants primarily subsist as browsers and/or frugivores. Ruminants, in contrast to hindgut fermenters, are morphophysiologically limited in their daily intake due to their longer digestive retention times and passage rates (Beekman and Prins 1989; Clauss et al. 2003, 2010). The longer retention times help maximize the energy extracted by the microbial community in the gut from low quality forage, often grasses. These longer retention times, however, are better tolerated by larger rather than smaller bodied species. The innate capacity for larger bodied animals to tolerate forage of lower quality is a function of the mismatch between the nonlinear relationship of metabolic requirements (MR) and body mass (BM), MR $= 70$ BM$^{0.75}$, and the near-linear relationship of gut capacity (GC) and body mass, log GC $= 1.03$ log BM-0.94 (Demment and Van Soest 1985). Therefore, compared to larger species, ruminants of smaller body mass are more dependent on higher quality forage, and to satisfy their nutritional requirements, smaller herbivores forage on browse and fruits that are of higher quality more than they forage on grasses (Bell 1970, 1971; Jarman 1974).

Large herbivores also have to contend with differences in the physical demands of feeding on grasses versus browse. Grasses in general are more fibrous, i.e., they have a greater proportion of cell wall (cellulose and hemicellulose) to cell content, and have higher levels of abrasive components like silica (Kaiser et al. 2009). Therefore when compared to browsers, grazers tend to have bigger masseter muscles, larger and deeper angles of the jaw, broader muzzles, and longer masseteric fossa on the skull (Gordon and Illius 1988; Clauss et al. 2008; Hofmann et al. 2008; Janis et al. 2010).

Building on what we know from studies of large herbivores in Europe, North America, and Africa, this chapter explores patterns in the feeding preferences of different large herbivore species in South and Southeast Asia (SSEA). We classified species as *grazers* if they consumed primarily graminoids year-round, *browsers* if they consumed primarily non-graminoids year-round, and *mixed feeders* if they either switched between grazing and browsing or consumed both browse and grasses. The wide range in body mass of species in the large herbivore assemblage in SSEA, which is similar to the body mass range observed in the large herbivore assemblage in Africa, allows us to analyze broad trends in foraging preferences as related to body mass and digestive syndromes.

One significant difference between the herbivore assemblages found in SSEA and Africa is that while there is only one Cervid (deer) species within the assemblage of 94 large herbivore species found in Africa (the Atlas deer *Cervus elaphas barbarus* found in the Atlas mountains in Africa's extreme Northwest), ∼30 % of large herbivore species that inhabit SSEA are Cervid species. It is, however, unclear how Bovids and Cervids differ in their digestive physiology and therefore, species of both groups were grouped together for our analysis (Langvatn and Hanley 1993; Hobbs et al. 1996; Mysterud 2000; Seagle 2003; Hewison et al. 2009; Beguin et al. 2011; Redjadj et al. 2014). Although pig species (Suidae) are sometimes included in analyses related to large herbivore forage selection, they are indeed omnivores and were therefore excluded from this study (Rerat 1978). Excluding the 13 suid species, we were left with 70 large herbivore species to analyze: six belonging to the order Perissodactyla, one belonging to the order Proboscidea (the Asian elephant), and the remaining 63 species (∼90 %) are ruminants and belong to the order Artiodactyla.

4.2 Forage Preference—Body Mass, Roughage, and Vegetation Quality

Given the paucity of data on forage preferences of many large herbivore species in SSEA, we pooled data and classified species in related groups, primarily by genus (Table 4.1). In general, forage selection by large herbivores is guided by the body mass of a species, its anatomical and morphological specializations, and the quantity, quality (mainly nitrogen and phosphorus), and the composition (level of roughage) of plant material (Bell 1971; Jarman 1974; Gordon and Illius 1996). In addition, the ratio of the abundance of grasses and browse at local scales influences the composition of a large herbivore assemblage found in a given area (Gordon 2003; Prins and Van Langevelde 2008; Owen-Smith 2014). In the savannas of Africa, for example, where browse is generally patchily distributed among vast grasslands, grazers dominate the large herbivore assemblage (Mcnaughton and Georgiadis 1986). In contrast, in tropical Asia where grasslands are patchily distributed within forested landscapes, mixed feeders should dominate the large herbivore assemblage. As expected, the majority of large herbivore species in SSEA

Table 4.1 Feeding preferences of groups of large herbivore species in Asia listed by order, family, and genus

Order, family	Species (common name)	Feeding type	Comments	References
Artiodactyla, Bovidae	*Antilope cervicapra* (blackbuck)	Grazer	The blackbuck is primarily a grazer throughout the year, even during periods when grasses have low nutrition. They appear to have evolved to occupy feeding niches in predominantly dry grassland landscapes	Jhala (1997), Isvaran (2007)
	Gazella bennettii (chinkara) *Gazella subgutturosa* (goitered gazelle)	Mixed feeders	These species are also found primarily in arid systems though the chinkara inhabits areas that are lower in elevation, latitude, but higher in temperature than the goitered gazelle. While it is unclear what the proportion of browse and grasses is in the diets of these species, and whether these proportions change seasonally, we know that the small body mass of this species has low quantity, but high quality nutritional requirements. These species, therefore, need to select for high-quality forage, but their arid habitats constrain available forage choices. Studies of gazelles in Africa have shown that the Grant's gazelle is primarily a browser, while the Thomson's gazelle is primarily a grazer (Cerling et al. 2003)	*chinkara*: Bagchi et al. (2003a, b) *goitered gazelle*: Xu et al. (2008, 2012)

Table 4.1 (continued)

Order, family	Species (common name)	Feeding type	Comments	References
	Bos gaurus (gaur) *Bos javanicus* (banteng) *Bos mutus* (yak) *Bos sauveli* (kouprey)	Grazers	Among all the ruminants that inhabit Asia, the four species that belong to the large body mass genus *Bos* best exemplify roughage feeders. The *Bos* species are endemic to Asia and the size of their rumens allows maximizing both fiber digestibility and the extraction of energy from a predominantly graminoid diet, especially when graminoids are phenologically old and dry (roughage). These species, however, do browse (for e.g., the gaur has been recorded feeding on numerous browse species including bark of trees), primarily during the dry season	*gaur*: Schaller (1967), Chetri (2003), Gad and Shyama (2011), Ahrestani et al. (2012) *banteng*: Matsubayashi et al. (2007) *yak & kouprey*: Data deficient
	Bubalus arnee (wild buffalo) *Bubalus depressicornis/quarlesi* (anoa) *Bubalus mindorensis* (tamaraw)	Grazers	The lack of field data on the wild buffalo means that the best information available for this species is based on the domestic buffalo, which is primarily a grazer. The wild buffalo has a body mass similar to species of the genus *Bos* and based on observations of domestic buffalo can be classified as a roughage feeder. The range of body mass among the three *Bubalus* species, however, is large (tamaraw: 200 kg–buffalo: 600 kg), and therefore the diets of the species would vary with respect to the proportion of browse in the diet, most probably increasing with decreasing body mass	Data deficient

Table 4.1 (continued)

Order, family	Species (common name)	Feeding type	Comments	References
	Boselaphus tragocamelus (nilgai)	Mixed feeder	The nilgai, a species monotypic within its genus, is the world's oldest extant tropical bovid species and the largest antelope species in Asia. It has been reported to be a mixed feeder consistent with what its premaxillary shape suggests. Its diet varies seasonally and includes graminoids, woody vegetation, forbs, sedges, and fruits (for e.g., 34 plant species have been known to germinate from nilgai feces in Keoladeo National Park, India)	Bagchi et al. (2003a, b), Solanki and Naik (1998) Khan (1994), Leslie (2008)
	Tetracerus quadricornis (four-horned antelope)	Mixed feeder	Like the Nilgai, the four-horned antelope is another species monotypic within its genus. It is believed to be a concentrate feeder with a wide latitudinal range and occupies open habitats with low tree density. Its habitat is more forested than that occupied by Asia's gazelles and blackbuck, which hints at its mixed feeder status	Krishna et al. (2009), Leslie and Sharma (2009), Baskaran et al. (2011)
	Capricornis spp. (mainland, red, southern and Himalayan)	Mixed feeders	Although there is data on the diet of the Japanese serow, which appears to be primarily a browser, no data exist for any of serow species in SSEA. Based on their habitat preferences, which includes both forests and grasslands, it is likely that the SSEA serow species are mixed foragers that vary their feeding seasonally, switching from graminoids in the wet season to browse in the dry season	Data deficient. There exists, however, data from other parts of Asia: Ochiai (1999), Song et al. (2005)

(continued)

Table 4.1 (continued)

Order, family	Species (common name)	Feeding type	Comments	References
	Capra spp. (markhor, ibex) Hemitragus spp. (tahr spp.) Naemorhedus spp. (goral spp.) Ovis ammon (argali) Pseudois nayaur (bharal) Budorcas taxicolor (takin)	Mixed feeders	In general sheep and goat species are considered opportunistic feeders that feed a lot on graminoids, but also on forbs and woody plants. Among all the large herbivore species found in SSEA, these species inhabit the highest altitude regions, which are relatively arid. The extreme seasonal variation in climate and forage availability that these species experience is probably the main reason why they are generalists rather than specialist feeders. Although the takin has been found to be a generalist, it prefers to browse	bharal: Mishra et al. (2004), Suryawanshi et al. (2010) argali: Namgail et al. (2004), Singh et al. (2010), Wingard et al. (2011) goral: Fakhar-I-Abbas et al. (2008) takin: Schaller et al. (1986)
Artiodactyla, Cervidae	Axis axis (chital) Axis porcinus (hog deer) Axis calamianensis (Calamian deer) Axis kuhlii (Bawean deer)	Mixed feeders	These species primarily feed on grasses during the wet season and have been found to switch to browse during the dry season, presumably when levels of protein in graminoids are too low to support their nutritional needs. These species generally occupy open forested habitats, and are not found in wet forests with little to no grasses in the understory. Although these species graze a lot, they are more selective of which plant parts they consume when compared to the sympatric larger (Cervid) Rusa species	chital: Moe and Wegge (1997), Ahrestani et al. (2012) hog deer: Dhungel and Ogara (1991), Odden et al. (2005), Wegge et al. (2006)

Table 4.1 (continued)

Order, family	Species (common name)	Feeding type	Comments	References
	Muntiacus spp. (muntjac spp.)	Mixed feeders	Although these species forage on both grasses and browse, they do so selectively. They are concentrate feeders that select primarily leafy components, often fruit, and ingest very little fibrous forage	Data deficient
	Recervus duvaucelii (swamp deer) *Recervus eldii* (Eld's deer)	Mixed feeders	Both these species are associated with swampy habitat where they feed primarily on grasses, aquatic shrubs, forbs, and sedges	Schaller (1967)
	Rusa unicolor (sambar) *Rusa timorensis* (rusa) *Rusa alfredi/marianna* (Philippine sambar spp.)	Mixed feeders	Occupying a diverse set of habitats, the sambar is the most widely distributed large herbivore species in Asia. Its wide range hints at a generalist feeding strategy, which recent studies seem to suggest is the case. The *Rusa* species are often found in dense forest, a habitat where grasses are normally not abundant and are patchily distributed. In such habitats, *Rusa* species have been found to be primarily browsers	*sambar*: Schaller (1967), Johnsingh and Sankar (1991), Padmalal et al. (2003), Bagchi et al. (2003a, b), Ahrestani et al. (2012)
Artiodactyla, Tragulidae	*Tragulus/Moschiola spp.* (chevrotain spp.)	Browsers	The concentrate feeder label would probably best describe the feeding habits of these species, as the small size of the rumens of these species demand that fibrous forage levels be kept to a bare minimum While not much is known about Asian species, the African chevrotain is understood to eat mainly fallen fruit	Matsubayashi et al. (2003)

(continued)

Table 4.1 (continued)

Order, family	Species (common name)	Feeding type	Comments	References
Artiodactyla, Moschidae	*Moschus spp.* (musk deer)	Mixed feeders	In general, little detailed information exists of these species. However, given that they occupy high altitude habitats that experience extreme seasonality, observations seem to suggest that musk deer are mixed feeders that forage primarily on grasses in alpine meadows in summer, and then more on shrubs, forbs, and lichen in winter	Data deficient
Perrisodactyla, Equidae	*Equus hemionus* (Indian wild ass) *Equus kiang* (kiang)	Grazers	These hindgut fermenters have digestive physiologies with low fermentation rates and digestive efficiencies that lead to short digestion passage times, which allow these species to have high consumption rates and deal with forage with high levels of roughage. Despite the lack of field data on these Asian species, data from their close relatives—the zebras in Africa—suggest that they should be grazers, which field observations seem to corroborate. Both the Asian species are found in semidesert or desert habitats, albeit at contrasting latitudes and altitudes. At present, it remains unknown if they satisfy their nutritional requirements by eating only grasses	Data deficient

Table 4.1 (continued)

| Order, family	Species (common name)	Feeding type	Comments	References
Perrisodactyla, Rhinocerotidae	*Rhinoceros unicornis* (Indian)	Grazer	Reflective of their feeding habits, the Javan and Sumatran species inhabit dense forest habitats, while the Indian rhino inhabits terrain that has extensive grasslands. Given that their ranges overlapped historically, it is possible that their forage preferences have resulted from resource partitioning as a means to avoid competition in the past	Dinerstein (1991), Pradhan et al. (2008)
	Rhinoceros sondaicus (Javan)	Browser		
	Dicerorhinus sumatrensis (Sumatran)	Browser		
Perrisodactyla, Tapiridae	*Tapirus indicus* (Asian tapir)	Mixed feeder	One of only four global tapir species, and the only one found in Asia, the Asian tapir is confined to dense tropical forests in SE Asia. Given its relatively high quantity forage requirements as a result of its large body mass, it is likely that the tapir is a generalist and a mixed feeder	Data deficient
Proboscidea, Elephantidae	*Elephas maximus* (Asian elephant)	Mixed feeder	Roughage feeders that forage on a wide variety of plant species, which maybe necessary to satisfy their high quantity requirements. Their hindgut fermentation trait syndroms provide short digestion passage rates, which enables them to tolerate high levels of roughage	Sukumar (1990, 1992), Matsubayashi et al. (2006), Pradhan et al. (2008), Ahrestani et al. (2012)
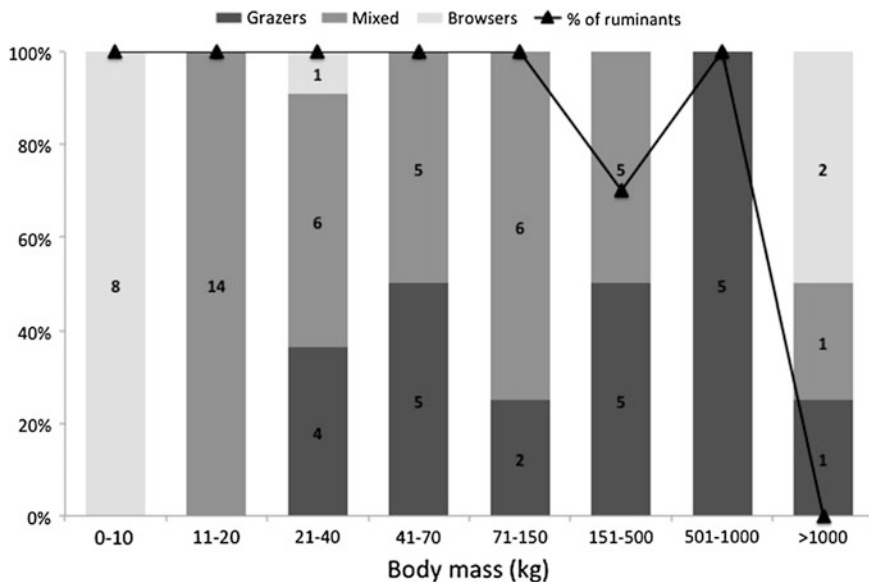
Fig. 4.1 Proportions of 70 large herbivore species found in South and Southeast Asia that are grazers (often bulk foragers), mixed feeders (that utilize both grasses and browse species), and browsers (often concentrate feeders) plotted in relation to body mass. The *line plots* the percentage of species that are ruminants in each body mass class. Numbers within *bars* denote the number of species of grazers, mixed feeders, or browsers in each body mass class. Although the 13 pig species found in the region are in the overall list of large herbivores for the region (see Chapter 1), they are indeed omnivores and were therefore excluded from this analysis

are mixed feeders (Fig. 4.1). However, concentrate feeders (browsers) dominate the smallest size categories, while bulk feeders, predominantly grazers, dominate the largest size categories (>500 kg, Fig. 4.1).

Studies of large herbivore assemblages in other regions have reported that browsers are found across the entire body size range of herbivores (Sponheimer et al. 2003). This is true for the assemblage in SSEA as well—ruminant browsers dominate the lowest body mass classes (Fig. 4.1), while the browsers in the largest body mass class are nonruminants (see Sect. 4.3 for more details). In SSEA, the smallest species are almost exclusively concentrate feeders and primarily frugivores (Fig. 4.1, Table 4.1) and typically occupy forested habitats. For example, the small muntjac and mouse deer species are selective with everything they feed on, selecting leaves and not stems when grazing, and selecting leaves, buds, and flowers when browsing (Barrette 1977). Mouse deer, classified as browsers, are probably the most selective of large herbivore species in SSEA, and represent a distinct frugi-folivore category (Bodmer 1990; Kingdon et al. 2013). They are similar in body mass to the smallest ruminant species found in Africa, the dik-diks, which are known to be concentrate feeders (Manser and Brotherton 1995; Dehority and Odenyo 2003; Kingdon et al. 2013). The tendency for smaller ruminants to be

browsers has been previously noted (Case 1979; Gordon and Illius 1994; Clauss et al. 2003), and the increased reliance on high-quality fruits in the smallest bodied species is potentially a consequence of their relatively greater metabolic demands (Bodmer 1990).

The mesoherbivore body mass class (50–500 kg) was comprised primarily of mixed feeders (Fig. 4.1), including both Bovid and Cervid species. Although Fig. 4.1 depicts a low percentage of browsers in the intermediate body mass range, this can be deceiving as many of the mixed feeders in the intermediate body mass categories browse extensively, just not exclusively, like for example, the ubiquitous sambar *Rusa unicolor* (Padmalal et al. 2003; Ahrestani et al. 2012). However, other Cervids such as the chital *Axis axis* appear to adopt a mixed-feeding strategy. For example, chital *Axis axis* in South India were found to graze during the wet season, but then switched to browse during the middle-late dry season (Ahrestani et al. 2012)—the bottleneck period when rainfall is practically nonexistent, graminoid growth is dormant, and grasses have their highest levels of roughage and lowest levels of nutrients (Scoones 1995; Drescher et al. 2006). At present, however, it is unclear which factors regulate the extent to which different mesoherbivore species in SSEA rely on browse relative to graze, and how this changes with body mass, season, and across environmental and vegetation gradients.

While concentrate feeding is confined to the smaller animals, bulk feeding, primarily of grasses, is confined to larger bovid species that are ruminants and equid species that are hindgut fermenters (Fig. 4.1). In general, grazing is more common among species with larger body mass, and in Africa's large herbivore assemblage, grazing ruminants are larger than browsing ruminants (Bell 1971; Case 1979; Bodmer 1990; Van Wieren 1996; Perez-Barberia et al. 2001). It has been argued that the tendency for larger ruminants to be grazers rather than browsers is not a consequence of physiological or digestive limitations (Gordon and Illius 1994), but rather a result of limitations imposed by forage availability and abundance (Van Soest 1994; Clauss et al. 2003). Given their large metabolic requirements, it is easier for large-bodied species to meet their daily forage requirements by consuming grasses that are often more abundantly available than browse (Clauss et al. 2003). However, when browse is available in abundance, browsing ruminants can achieve large body sizes as in the case of moose *Alces alces* and giraffe *Giraffa camelopardalis* (Clauss et al. 2003).

The majority of large-bodied species in SSEA are wild Bovini species, i.e., species belonging to the genus *Bos,* which are similar to domestic cattle and are primarily grazers. Because of their low metabolic requirement to gut capacity ratio, these large Bovini species are able to tolerate high levels of roughage. However, wild Bovini species that inhabit forests, like the gaur and banteng, have been recorded browsing on multiple plant species (Schaller 1967). Gaur have also been observed eating the bark of trees during the dry season (Pasha et al. 2002), which could be related to the lack of nutrition in tropical deciduous forests during the dry season (Ahrestani et al. 2011). The many observations of Bovini species migrating

to low-lying regions near rivers and drainage lines during the dry season seem to suggest that these wetter habitats—that typically retain a herbaceous layer in the dry season—act as key foraging habitats for species like the gaur in the dry season (Conry 1989; Ahrestani and Karanth 2014; Prins and Van Oeveren 2014).

4.3 Digestive Physiology Trait Syndromes: Hindgut versus Foregut

The distribution of foregut and hindgut fermenters across the body mass gradient of the large herbivore assemblage in SSEA (2–3070 kg) is illustrated in Fig. 4.1. There is a complete absence of hindgut fermenters in the lower body mass classes and a complete absence of ruminants in the megaherbivore class (>1000 kg). In general, the global megaherbivore guild is dominated by hindgut fermenters except for the giraffe *Giraffa camelopardalis* and hippopotami *Hippopotamus sp.* and it has been argued that the foregut digestive trait syndrome is not the most efficient for species with body mass >1000 kg (Demment and Van Soest 1985; Clauss et al. 2003).

Compared to ruminants, hindgut fermenters can tolerate forage of lower quality primarily because of lower retention times and faster passage rates in their digestive trait syndromes (Van Soest 1994). Their higher faster rates also allow hindgut fermenters to achieve larger body sizes than ruminants. All four megaherbivores in Asia (the Asian elephant and the Sumatran, Javan and Indian rhinoceros) are hindgut fermenters. The Asian elephant is a mixed feeder that consumes both browse and grass throughout the year, or follows a foraging regime that switches between dry season browsing and wet season grazing (Sukumar 1990, 1992). Despite being a mixed and bulk forager—a foraging strategy that is probably necessary to satisfy the metabolic requirements of over three tonnes of body mass— it is possible that the Asian elephant is selective in what it seasonally eats in some areas, similar to what the African elephant does in areas where nutrient levels vary significantly among forage species (Woolley et al. 2009; Owen-Smith and Chafota 2012; Pretorius et al. 2012).

Amongst the rhinocerotids, the Indian rhinoceros *Rhinoceros unicornis* (the Indian rhino) "is a semi-hypsodont, and is able to graze", while the closely related *R. sondaicus* (the Javan rhino) and the more distantly related *Dicerorhinus suma-trensis* (the Sumatran rhino) are brachydont browsers (Prothero et al. 1989). The two lineages (*Rhinoceros* and *Dicerorhinus*) have been present in SSEA since the Pliocene, and *R. sondaicus* appears to be a more recent species than *R. unicornis* (Prothero et al. 1989; De Iongh et al. 2005, also see Chap. 2). The contrast-ing feeding strategies of the Asian rhinoceros species bear similarities to their African counterparts. The two rhino species in Africa, though possessing similar hindgut digestive trait syndromes, have contrasting diets; the white rhino

Ceratotherium simum is more or less an exclusive grazer and the black rhino *Diceros bicornis* is more or less an exclusive browser (Owen-Smith 1992; Luske et al. 2009; Van Lieverloo et al. 2009). A similar scenario was also present in the North American Micocene ungulate assemblage (Prothero et al. 1989), which had one grazing rhino species sympatric with one browsing rhino species.

Only three hindgut fermenter species below 500 kg inhabit SSEA: two *Equus spp*. (Asiatic and the Tibetan wild ass) that are both grazers, and the Asian tapir that is considered a mixed feeder. Both *Equus* species inhabit dry habitats characterised by sparse and patchily distributed forage of poor quality, conditions that are better handled by hindgut rather than foregut fermentation trait syndromes (Clauss et al. 2003). In contrast to the dry habitats of the *Equus*, the Asian tapir, inhabits mainly moist forests and often rainforests (Clements et al. 2012; Table 4.1). In general, except for its frugivorous habits (Campos-Arceiz et al. 2012), little else is known about the diet of Asian tapir. The other three tapir species in the world are all found in Central and South America, where they often inhabit forests (Fragoso 1997; Galetti et al. 2001). In general, forests do not support high levels of graminoid production and the morphology of the tapir's snout suggests an evolutionary adaptation to frugivory and browsing (Janis 1984; Milewski and Dierenfeld 2013). Much of the research on the tapir species in Central and South America has focused on frugivory, which has shown that the diets of these species in forests, lowland river basins, and marshlands are extremely diverse and include more than 100 plant species (Salas and Fuller 1996; Lizcano and Cavelier 2000; Downer 2001; Tobler 2002; Chalukian et al. 2013).

4.4 Body Size and Habitat Associations

Of the ruminants, members of the Tragulidae and Moschidae are restricted to the smallest size classes, in contrast to the Cervids and Bovids that have larger body mass ranges (Fig. 4.2). Cervids in SSEA do not appear to get as large as Bovids (Fig. 4.2) and in both Cervids and Bovids, the greatest number of species are found in the smaller body mass classes (Fig. 4.2). The largest Cervid in Asia—the Kashmir stag, *Cervus elaphus hanglu*, a species that shares its genus and species lineage with the only deer species found in Africa, the barbary stag *Cervus elaphus barbarus*—has a body mass comparable to the body mass of the *Equus spp*. in Asia; all other Cervid species in Asia are smaller. The nonruminants of SSEA are much larger (>150 kg) with 4 of the 7 nonruminants falling within the megaherbivore category.

Although large herbivores in SSEA occupy a range of different habitats from arid grasslands to rainforests, there are discernible habitat associations within different groups. Tragulids and Moschids, which are predominantly browsers and frugivores, are restricted to forested habitats. Cervids and Bovids occur in a wide

Fig. 4.2 The species of four families of the order Artiodactyla (*M* Moschidae (5 species), *T* Tragulidae (8 species), *C* Cervidae (20 species), *B* Bovidae (30 species)) found in South and Southeast Asia distributed by body mass
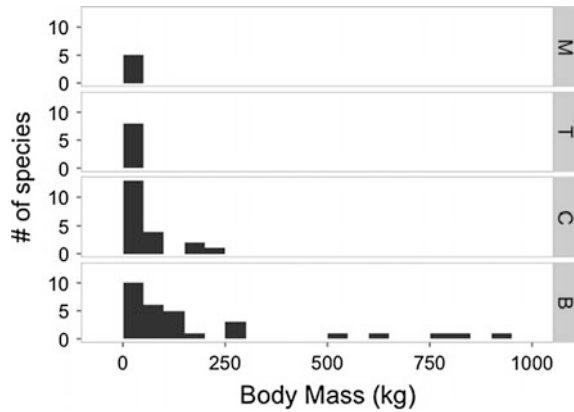
array of different habitat types, although the habitat ranges of Cervids tend to be more restricted than those of Bovides. In general, Cervids are nearly never found in extreme dry habitats, presumably because of their greater dependence on moisture when compared to Bovids. Among nonruminants, the Equids are restricted to arid habitats, the single Tapirid to forests and river basins, the Rhinocerotids to forests and grasslands, while the Asian elephant occurs in a range of habitats from tall grasslands to savannas to forests.

The only ruminant found in the dry and hot landscape that the Indian wild ass *Equus hemionus* inhabits, is the chinkara *Gazella benetti*. The chinkara, <20 kg, is smaller by an order of magnitude when compared to the wild ass, ~200 kg, which is a non-ruminant. Constraints imposed by the sparse and patchily distributed forage in these hot and dry habitats seem to allow only the smallest ruminants to persist in these inhospitable habitats. In contrast to the low number of species inhabiting extremely hot and dry habitats, the kiang *Equus kiang*, which inhabits dry and cold high altitude terrain that supports only sparse and patchily distributed forage in conditions of extreme seasonality, is sympatric with multiple ruminant species: mountain goat and sheep species that are generally mixed feeders, and the larger yak, a Bovini species that is considered a grazer. Cold and dry habitats in SSEA, therefore, support a more diverse ruminant assemblage when compared to hot and dry habitats.

4.5 Conclusions and Future Directions

The foraging preferences exhibited by large herbivore species in SSEA, especially at the extreme ends of the body mass gradient, suggest that body mass plays a role in shaping the forage preference of these species (Fig. 4.1). Additionally, the absence of ruminants from the megaherbivore class in this assemblage supports the proposition that the foregut trait syndrome does not commonly support body mass

>1000 kg (Van Soest 1994; Clauss et al. 2003). Existing data suggest that Cervid species in Asia are predominantly mixed feeders, some throughout the year and others seasonally, and that the level of concentrate feeding by deer species increases with decreasing body mass (Table 4.1). The majority of Bovid species <200 kg are mixed feeders too, and the largest Bovids (wild cattle >500 kg) are roughage feeders of primarily grasses (Table 4.1).

From Table 4.1, we see that there is an acute lack of data on the foraging ecology of the majority of large herbivore species in SSEA. The framework—based on interacting causal factors of body mass, digestive trait syndromes, and habitat heterogeneity—that helped understand patterns observed in the foraging by large herbivore assemblages in Africa was established nearly half a century ago (Bell 1970, 1971; Jarman 1974). That framework, however, has yet to be fully tested on a large herbivore assemblage in SSEA. In general, classifying large herbivores either as grazers, browsers, or mixed feeders helps us understand their foraging ecology. However, the seasonal variation in the levels of available nutrients, roughage, and quantity in plant material ultimately determines what a large herbivore consumes over space and time, and forage selection is directed by a complex set of drivers that does not allow for a distinct optimal prediction (Hanley 1982). In the context of prevailing global change, understanding these mechanisms has got a lot more challenging as bush encroachment further modifies grasslands (Mitchard and Flintrop 2013) and increased levels of CO_2 can potentially change the distribution of C_3 and C_4 grasses and woody vegetation worldwide (Chamaille-Jammes and Bond 2010). Finally, though natural history descriptions began in SSEA more than a century ago, it is imperative that ecological research increases in the region as SSEA seriously lags behind in understanding the fundamentals of its natural heritage.

References

Ahrestani FS, Karanth KU (2014) Gaur (Bos gaurus Smith CH, 1827). In: Melletti M, Burton J (eds) Ecology, evolution and behaviour of wild cattle. Cambridge University Press, Cambridge, pp 174–193

Ahrestani FS, Heitkonig IMA, Prins HHT (2011) Herbaceous production in South India-limiting factors and implications for large herbivores. Plant Soil 349:319–330

Ahrestani FS, Heitkonig IMA, Prins HHT (2012) Diet and habitat-niche relationships within an assemblage of large herbivores in a seasonal tropical forest. J Trop Ecol 28:385–394

Bagchi S, Goyal SP, Sankar K (2003a) Habitat separation among ungulates in dry tropical forests of Ranthambhore National Park Rajasthan. Trop Ecol 44:175–181

Bagchi S, Goyal SP, Sankar K (2003b) Niche relationships of an ungulate assemblage in a dry tropical forest. J Mammal 84:981–988

Barrette C (1977) Some aspects of the behaviour of muntjacs in Wilpattu National Park. Mammalia 41:1–34

Baskaran N, Kannan V, Thiyagesan K et al (2011) Behavioural ecology of four-horned antelope (Tetracerus quadricornis de Blainville, 1816) in the tropical forests of southern India. Mamm Biol 76:741–747

Beekman JH, Prins HHT (1989) Feeding strategies of sedentary large herbivores in East Africa, whith emphasis on the African buffalo, Syncerus caffer. Afr J Ecol 27:129–147

Beguin J, Pothier D, Cote SD (2011) Deer browsing and soil disturbance induce cascading effects on plant communities: a multilevel path analysis. Ecol Appl 21:439–451

Bell RHV (1970) The use of the herb layer by grazing ungulates in the Serengeti. In: Watson A (ed) Animal populations in relation to their food resources, tenth symposium of tile British ecological society. Blackwell Scientific Publications, Oxford, pp 111–123

Bell RHV (1971) Grazing ecosystem in serengeti. Sci Am 225:86

Bodmer RE (1990) Ungulate frugivores and the browser-grazer continuum. Oikos 319–325

Bodmer R, Ward D (2006) Frugivory in large mammalian herbivores. In: Danell K, Duncan P, Bergström R, Pastor J (eds) Large herbivore ecosystem dynamics and conservation. Cambridge University Press, Cambridge, pp 232–260

Bouchenak-Khelladi Y, Verboom GA, Hodkinson TR et al (2009) The origins and diversification of C-4 grasses and savanna-adapted ungulates. Glob Change Biol 15:2397–2417

Campos-Arceiz A, Traeholt C, Jaffar R et al (2012) Asian tapirs are no elephants when it comes to seed dispersal. Biotropica 44:220–227

Case TJ (1979) Optimal body size and an animal's diet. Acta Biotheor 28:54–69

Cerling TE, Wang Y, Quade J (1993) Expansion of C4 ecosystems as an indicator of global ecological change in the late Miocene. Nature 361:344–345

Cerling TE, Harris JM, Macfadden BJ et al (1997) Global vegetation change through the Miocene/Pliocene boundary. Nature 389:153–158

Cerling TE, Harris JM, Passey BH (2003) Diets of east african bovidae based on stable isotope analysis. J Mammal 84:456–470

Chalukian SC, Soledad De Bustos M, Leonidas Lizarraga R (2013) Diet of lowland tapir (Tapirus terrestris) in El Rey National Park, Salta, Argentina. Integr Zool 8:48–56

Chamaille-Jammes S, Bond WJ (2010) Will global change improve grazing quality of grasslands? A call for a deeper understanding of the effects of shifts from C-4 to C-3 grasses for large herbivores. Oikos 119:1857–1861

Chetri M (2003) Food habits of gaur (Bos gaurus) and livestock (cows and buffaloes) in Parsa Wildlife Sanctuary, central Nepal. Himalayan J Sci 1:31–36

Clauss M, Frey R, Kiefer B et al (2003) The maximum attainable body size of herbivorous mammals: morphophysiological constraints on foregut, and adaptations of hindgut fermenters. Oecologia 136:14–27

Clauss M, Hofmann RR, Streich WJ et al (2008) Higher masseter muscle mass in grazing than in browsing ruminants. Oecologia 157:377–385

Clauss M, Hofmann RR, Streich WJ et al (2010) Convergence in the macroscopic anatomy of the reticulum in wild ruminant species of different feeding types and a new resulting hypothesis on reticular function. J Zool 281:26–38

Clements GR, Rayan DM, Aziz SA et al (2012) Predicting the distribution of the Asian tapir in Peninsular Malaysia using maximum entropy modeling. Integr Zool 7:400–406

Conry PJ (1989) Gaur (Bos gaurus) and development in Malaysia. Biol Conserv 49:47–65

Damuth J, Janis CM (2011) On the relationship between hypsodonty and feeding ecology in ungulate mammals, and its utility in palaeoecology. Biol Rev 86:733–758

De Iongh HH, Prins HHT, Van Strien N et al (2005) Some observations on the presence of one-horned rhinos in the bas reliefs of the Ankor Wat temple complex. Pachyderm 96–100

Dehority BA, Odenyo AA (2003) Influence of diet on the rumen protozoal fauna of indigenous African wild ruminants. J Eukaryot Microbiol 50:220–223

Demment MW, Van Soest PJ (1985) A nutritional explanation for body-size patterns of ruminants and nonruminant herbivores. Am Nat 125:641–672

Dhungel SK, Ogara BW (1991) Ecology of the hog deer in Royal Chitwan National Park, Nepal. Wildlife Monographs 1–40

Dinerstein E (1991) Seed dispersal by greater one-horned rhinoceros (Rhinoceros unicornis) and the flora of rhinoceros latrines. Mammalia 55:355–362

Downer CC (2001) Observations on the diet and habitat of the mountain tapir (Tapirus pinchaque). J Zool 254:279–291

Drescher M, Heitkonig IMA, Van Den Brink PJ et al (2006) Effects of sward structure on herbivore foraging behaviour in a South African savanna: an investigation of the forage maturation hypothesis. Aust Ecol 31:76–87

Duncan AJ, Poppi DP (2008) Nutritional ecology of grazing and browsing ruminants. In: Gordon IJ, Prins HHT (eds) Ecology of browsing and grazing. Springer, Berlin, pp 89–116

Fakhar-I-Abbas F, Akhtar T, Mian A (2008) Food and feeding preferences of Himalayan gray goral (Naemorhedus goral bedfordi) in Pakistan and Azad Jammu and Kashmir. Zoo Biol 27:371–380

Fragoso JMV (1997) Tapir-generated seed shadows: scale-dependent patchiness in the Amazon rain forest. J Ecol 85:519–529

Gad SD, Shyama SK (2011) Diet composition and quality in Indian bison (Bos gaurus) based on fecal analysis. Zoolog Sci 28:264–267

Galetti M, Keuroghlian A, Hanada L et al (2001) Frugivory and seed dispersal by the lowland tapir (Tapirus terrestris) in southeast Brazil. Biotropica 33:723–726

Gordon IJ (2003) Browsing and grazing ruminants: are they different beasts? For Ecol Manage 181:13–21

Gordon IJ, Illius AW (1988) Incisor arcade structure and diet selection in ruminants. Funct Ecol 2:15–22

Gordon IJ, Illius AW (1994) The functional significance of the browser-grazer dichotomy in African ruminants. Oecologia 98:167–175

Gordon IJ, Illius AW (1996) The nutritional ecology of African ruminants: a reinterpretation. J Anim Ecol 65:18–28

Hanley TA (1982) The nutritional basis for food selection by ungulates. J Range Manag 35:146–151

Hewison AJM, Morellet N, Verheyden H et al (2009) Landscape fragmentation influences winter body mass of roe deer. Ecography 32:1062–1070

Hobbs NT, Baker DL, Bear GD et al (1996) Ungulate grazing in sagebrush grassland: mechanisms of resource competition. Ecol Appl 6:200–217

Hofmann RR, Stewart DRM (1972) Grazer and browser: a classification based on the stomach-structure and feeding habits of East African ruminants. Mammalia 36:226–240

Hofmann RR (1973) The ruminant stomach (stomach structure and feeding habits of East African game ruminants). East Afr Monogr Biol 2:1–364

Hofmann RR (1989) Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. Oecologia 78:443–457

Hofmann RR, Streich WJ, Fickel J et al (2008) Convergent evolution in feeding types: salivary gland mass differences in wild ruminant species. J Morphol 269:240–257

Isvaran K (2007) Intraspecific variation in group size in the blackbuck antelope: the roles of habitat structure and forage at different spatial scales. Oecologia 154:435–444

Janis C (1984) Tapirs as living fossils. In: Eldredge N, Stanley SM (eds) Living fossils. Springer, New York, pp 80–86

Janis C (2008) An evolutionary history of browsing and grazing ungulates. In: Gordon IJ, Prins HHT (eds) Ecology of browsing and grazing. Springer, Berlin, pp 21–45

Janis CM, Constable EC, Houpt KA et al (2010) Comparative ingestive mastication in domestic horses and cattle: a pilot investigation. J Anim Physiol Anim Nutr 94:E402–E409

Jarman PJ (1974) Social organization of antelope in relation to their ecology. Behaviour 48:215

Jhala YV (1997) Seasonal effects on the nutritional ecology of blackbuck Antelope cervicapra. J Appl Ecol 34:1348–1358

Johnsingh AJT, Sankar K (1991) Food plants of chital, sambar and cattle on Mundunthurai plateau, Tamil Nadu, South India. Mammalia 55:57–66

Kaiser TM, Brasch J, Castell JC et al (2009) Tooth wear in captive wild ruminant species differs from that of free-ranging conspecifics. Mamm Biol 74:425–437

Khan JA (1994) Food habits of ungulates in dry tropical forests of Gir Lion Sanctuary, Gujarat, India. Acta Theriol 39:185–193

Kingdon J, Happold D, Butynski T et al (2013) Mammals of Africa (Volume VI) A&C Black

Krishna YC, Clyne PJ, Krishnaswamy J et al (2009) Distributional and ecological review of the four horned antelope, Tetracerus quadricornis. Mammalia 73:1–6

Langvatn R, Hanley TA (1993) Feeding-patch choice by red deer in relation to foraging efficiency—an experiment. Oecologia 95:164–170

Leslie DM (2008) Boselaphus tragocamelus (Artiodactyla: Bovidae). Mamm Species 813:1–16

Leslie DM, Sharma K (2009) Tetracerus quadricornis (Artiodactyla: Bovidae). Mamm Species 843:1–11

Lizcano DJ, Cavelier J (2000) Daily and seasonal activity of the mountain tapir (Tapirus pinchaque) in the Central Andes of Colombia. J Zool 252:429–435

Luske BL, Mertens T, Lent PC et al (2009) Impact of the black rhinoceros (Diceros bicornis minor) on a local population of Euphorbia bothae in the Great Fish River Reserve, South Africa. Afr J Ecol 47:509–517

Manser MB, Brotherton PNM (1995) Environmental constraints of the foraging behavior of a dwarf antelope (Madoqua kirkii). Oecologia 102:404–412

Matsubayashi H, Bosi E, Kohshima S (2003) Activity and habitat use of lesser mouse-deer (Tragulus javanicus). J Mammal 84:234–242

Matsubayashi H, Lagan P, Sukor JRA (2006) Utilization of Macaranga trees by Asian elephants (Elephas maximus) in Borneo. Mammal Study 115–118

Matsubayashi H, Lagan P, Sukor JRA (2007) Herbal seed dispersal by the banteng (Bos javanicus) in a Bornean tropical rain forest. Malayan Nat J 59:297–303

Mcnaughton SJ, Georgiadis NJ (1986) Ecology of African grazing and browsing mammals. Annu Rev Ecol Syst 17:39–65

Milewski AV, Dierenfeld ES (2013) Structural and functional comparison of the proboscis between tapirs and other extant and extinct vertebrates. Integr Zool 8:84–94

Mishra C, Van Wieren SE, Ketner P et al (2004) Competition between domestic livestock and wild bharal Pseudois nayaur in the Indian Trans-Himalaya. J Appl Ecol 41:344–354

Mitchard ETA, Flintrop CM (2013) Woody encroachment and forest degradation in sub-Saharan Africa's woodlands and savannas 1982–2006. Philos Trans R Soc B-Biol Sci 368

Moe SR, Wegge P (1997) The effects of cutting and burning on grass quality and axis deer (Axis axis) use of grassland in lowland Nepal. J Trop Ecol 13:279–292

Mysterud A (2000) Diet overlap among ruminants in Fennoscandia. Oecologia 124:130–137

Namgail T, Fox JL, Bhatnagar YV (2004) Habitat segregation between sympatric Tibetan argali Ovis ammon hodgsoni and blue sheep Pseudois nayaur in the Indian Trans-Himalaya. J Zool 262:57–63

Ochiai K (1999) Diet of the Japanese serow (Capricornis crispus) on the Shimokita Peninsula, northern Japan, in reference to variations with a 16-years interval. Mammal Study 24:91–102

Odden M, Wegge P, Storaas T (2005) Hog deer Axis porcinus need threatened tallgrass floodplains: a study of habitat selection in lowland Nepal. Anim Conserv 8:99–104

Owen-Smith N (1992) Megaherbivores. Cambridge University Press, Cambridge

Owen-Smith N (2014) Spatial ecology of large herbivore populations. Ecography 37:416–430

Owen-Smith N, Chafota J (2012) Selective feeding by a megaherbivore, the African elephant (Loxodonta africana). J Mammal 93:698–705

Padmalal U, Takatsuki S, Jayasekara P (2003) Food habits of sambar Cervus unicolor at the Horton Plains National Park, Sri Lanka. Ecol Res 18:775–782

Pasha MKS, Areendran G, Sankar K et al (2002) Debarking of teak Tectona grandis Linn. f. by gaur Bos gaurus H. Smith during summer in a tropical dry deciduous habitat of central India. J Bombay Nat Hist Soc 99:238–244

Perez-Barberia FJ, Gordon IJ, Nores C (2001) Evolutionary transitions among feeding styles and habitats in ungulates. Evol Ecol Res 3:221–230

Pradhan NMB, Wegge P, Moe SR et al (2008) Feeding ecology of two endangered sympatric megaherbivores: Asian elephant Elephas maximus and greater one-horned rhinoceros Rhinoceros unicornis in lowland Nepal. Wildl Biol 14:147–154

Pretorius Y, Stigter JD, De Boer WF et al (2012) Diet selection of African elephant over time shows changing optimization currency. Oikos 121:2110–2120

Prins HHT, Gordon IJ (2008) Grazers and browsers in a changing world. In: Gordon IJ, Prins HHT (eds) Ecology of browsing and grazing. Springer, Berlin, pp 1–20

Prins HHT, Olff H (1998) Species-richness of African grazer assemblages: towards a functional explanation. In: Newbery DM, Prins HHT, Brown ND (eds) Dynamics of tropical communities. British ecological society symposium, vol 37. Blackwell Science, Oxford, pp 449–490

Prins HHT, Van Langevelde F (2008) Assembling a diet from different places. In: Prins HHT, Van Langevelde F (eds) Resource ecology: spatial and temporal dynamics of foraging. Springer, Dordrecht, pp 129–158

Prins HHT, Van Oeveren H (2014) Bovini as keystone species and landscape architects. In: Melletti M, Burton J (eds) Ecology, evolution and behaviour of wild cattle. Cambridge University Press, Cambridge, pp 21–29

Prothero DR, Guérin C, Manning E (1989) The history of the Rhinocerotoidea. In: Prothero DR, Schoch RM (eds) The evolution of perissodactyls. Oxford University Press, Oxford

Redjadj C, Darmon G, Maillard D et al (2014) Intra- and interspecific differences in diet quality and composition in a large herbivore community. Plos One 9

Rerat A (1978) Digestion and absorption of carbohydrates and nitrogenous matters in the hindgut of the omnivorous nonruminant animal. J Anim Sci 46:1808–1837

Salas LA, Fuller TK (1996) Diet of the lowland tapir (Tapirus terrestris L) in the Tabaro River valley, southern Venezuela. Can J Zool-Revue Canadienne De Zoologie 74:1444–1451

Schaller GB (1967) The Deer and the Tiger: a study of wildlife in India. University of Chicago Press, Chicago

Schaller GB, Qitao T, Wenshi P et al (1986) Feeding behabior of Sichuan takin. Mammalia 50:311–322

Scoones I (1995) Exploiting heterogeneity—Habitat use in cattle in dyrland Zimbabwe. J Arid Environ 29:221–237

Seagle SW (2003) Can ungulates foraging in a multiple-use landscape alter forest nitrogen budgets? Oikos 103:230–234

Singh NJ, Yoccoz NG, Lecomte N et al (2010) Scale and selection of habitat and resources: Tibetan argali (Ovis ammon hodgsoni) in high-altitude rangelands. Can J Zool-Revue Canadienne De Zoologie 88:436–447

Solanki GS, Naik RM (1998) Grazing interactions between wild and domestic herbivores. Small Ruminant Res 27:231–235

Song Y-L, Gong H-S, Zeng Z-G et al (2005) Food habits of Serow. Chin J Zool 40:50–56

Sponheimer M, Lee-Thorp JA, DeRuiter DJ et al (2003) Diets of southern African Bovidae: Stable isotope evidence. J Mammal 84:471–479

Sukumar R (1990) Ecology of the Asian elephant in southern India. 2. Feeding habits and crop raiding patterns. J Trop Ecol 6:33–53

Sukumar R (1992) The Asian elephant: ecology and management. Cambridge University Press, Cambridge

Suryawanshi KR, Bhatnagar YV, Mishra C (2010) Why should a grazer browse? Livestock impact on winter resource use by bharal Pseudois nayaur. Oecologia 162:453–462

Tobler MW (2002) Habitat use and diet of Baird's tapirs (Tapirus bairdii) in a montane cloud forest of the Cordillera de Talamanca, Costa Rica. Biotropica 34:468–474

Van Lieverloo RJ, Schuiling BF, De Boer WF et al (2009) A comparison of faecal analysis with backtracking to determine the diet composition and species preference of the black rhinoceros (Diceros bicornis minor). Eur J Wildl Res 55:505–515

Van Soest PJ (1994) Nutritional ecology of the ruminant. Cornell University Press, Cornell

Van Wieren SE (1996) Browsers and grazers: foraging strategies in ruminants. Digestive strategies in ruminants and nonruminants 119–146

Wegge P, Shrestha AK, Moe SR (2006) Dry season diets of sympatric ungulates in lowland Nepal: competition and facilitation in alluvial tall grasslands. Ecol Res 21:698–706

Wingard GJ, Harris RB, Pletscher DH et al (2011) Argali food habits and dietary overlap with domestic livestock in Ikh Nart Nature Reserve, Mongolia. J Arid Environ 75:138–145

Woolley LA, Millspaugh JJ, Woods RJ et al (2009) Intraspecific strategic responses of African elephants to temporal variation in forage quality. J Wildl Manag 73:827–835

Xu W, Qiao J, Liu W et al (2008) Food habits of goitered gazelles (Gazella subgutturosa sairensis) in northern Xinjiang. Acta Theriologica Sinica 28:280–286

Xu W, Xia C, Lin J et al (2012) Diet of Gazella subgutturosa (Guldenstaedt, 1780) and food overlap with domestic sheep in Xinjiang, China. Folia Zool 61:54–60