

## 16

## Mesobrowser Abundance and Effects on Woody Plants in Savannas

David J. Augustine<sup>1</sup>, Peter Frank Scogings<sup>2</sup>, and Mahesh Sankaran<sup>3,4</sup>

<sup>1</sup>Rangeland Resources Research Unit, US Department of Agriculture – Agricultural Research Service, Fort Collins, CO, USA

<sup>2</sup>School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, South Africa

<sup>3</sup>National Centre for Biological Sciences, Tata Institute of Fundamental Research, Bangalore, Karnataka, India

<sup>4</sup>School of Biology, Faculty of Biological Sciences, University of Leeds, Leeds, UK

### 16.1 Introduction

Savannas, as defined in Chapter 1, are any formation with a C<sub>4</sub> grass understory and a woody canopy layer that has not reached a closed canopy state (Ratnam et al. 2011). Climate, soils, fire, and herbivory are widely recognized as four key drivers of the structure, composition, and functioning of savanna ecosystems. The relative role of these factors, and how they interact at varying spatial and temporal scales, has been the subject of an immense body of ecological literature. Continental-scale syntheses focused on these drivers show that climate and soils are primary determinants of woody vegetation abundance and species composition in savannas (Sankaran et al. 2008; Lehmann et al. 2014). However, at local spatial scales, fire and herbivory can regulate woody plant abundance below climatically determined maxima and alter plant growth rates, size class distributions, and community composition (e.g. Sankaran et al. 2013; Scholtz et al. 2014). Fire is well known to shape woody vegetation structure and composition in savannas worldwide (Lehmann et al. 2014), while less is known about the role of herbivores and the complex suite of factors that can regulate herbivore abundance and plant defenses (Chapter 15). Given that herbivore management strategies and land use patterns often strongly influence herbivores at local scales, an understanding of the consequences for savanna vegetation is needed to guide management and land use planning policies.

The most dramatic and visible effects of herbivores on woody plants occur in African savannas with elephants (*Loxodonta africana*), particularly where elephants have increased in density following movement restrictions or where iconic stands of large trees are experiencing elephant-induced mortality (e.g. Skarpe et al. 2004; Chapter 17 this volume). However, savannas support a guild of smaller browsing and mixed-feeding mammalian herbivores that vary widely in abundance, diversity, feeding niches, and

body size distribution. Here we focus on the direct effects of these mesobrowsers on woody plants in savannas, focusing on the class of mammalian ungulates and macropodids that range in size from approximately 5 kg (e.g. dik-dik, *Madoqua* spp.) to 1000 kg (e.g. eland, *Taurotragus* spp.), but which are mostly <500 kg. Excluded from this mesobrowser class are the megabrowsers, which range in size from giraffe (*Giraffa camelopardis*; 800–1200 kg) to African elephants (2500–6000 kg) and whose ecological role in savannas is strongly influenced by their size (Owen-Smith 1992). We use the term “mesobrowser” to refer to both mixed-feeding herbivores (species for which woody plants and herbaceous dicots comprise >50% of the diet on an annual basis) and species that predominantly consume browse. Although mixed-feeders typically consume substantial amounts of grass during wet seasons, they still consume and can substantially influence woody plant growth. Here, we review the distribution and abundance of mesobrowsers in savannas around the world. We then review long-term studies of the effects of mesobrowsers on woody plant growth and community dynamics, most of which have been conducted in African savannas. We seek to understand ecosystem-level characteristics that allow or prevent mesobrowser regulation of woody plant recruitment and growth rates, as both native and domestic mesobrowser abundance are influenced by human activities and management. Furthermore, debates surrounding elephant management in African savannas often center on how elephants are affecting woody plants, but knowledge of mesobrowser effects is essential to determine whether elephant management will achieve desired outcomes for savanna vegetation.

## 16.2 Mesobrowser Abundance in Savannas

Native mesobrowser abundance in tropical savannas varies dramatically among continents. Most notably, native mesobrowsers are rare or absent from Neotropical and Australasian savannas. The extensive and largely unmodified tropical savannas of northern Australia are characterized by extreme seasonality in precipitation (>85% occurring in the wet season, followed by >6 months of dry season), high levels of endemism in many components of the flora and fauna, but a general lack of large, mammalian herbivores (Bowman et al. 2010). The only widely distributed, large (>10 kg) native herbivores are the antilopine wallaroo (*Macropus antilopinus*) and common wallaroo (*M. robustus*), both of which occur at mean densities less than 10 km<sup>-2</sup> (Ritchie et al. 2008). The antilopine wallaroo, which is the more abundant of the two species (Ritchie et al. 2008), is almost exclusively a grazer (Dawson 1995). The common wallaroo is a mixed-feeder, but only occurs at densities <1 km<sup>-2</sup> across the region and is largely limited by dry season water availability, heat loads, predation, and low forage quality in these nutrient-poor savannas (Ritchie et al. 2008). As a result, browsing by macropodids is unlikely to be a primary factor shaping the structure and composition of these savannas. Some smaller, browsing arboreal mammals are also present in the region. Of note is the common brushtail possum (*Trichosurus velpecula*; 1–4 kg), which consumes *Eucalyptus* spp. foliage as a primary dietary component and whose reproductive performance can be strongly influenced by eucalypt secondary chemistry (DeGabriel et al. 2009). The influence of such arboreal folivores on woody vegetation dynamics in tropical savannas remains poorly studied, and is not considered further here.

As in the Australian savannas, mammalian mesobrowsers are generally absent or rare in Neotropical savannas. In the Cerrado of Brazil and Llanos of Venezuela, soils are severely leached, causing aluminum toxicity and low forage quality, and African grasses have been introduced to help support domestic livestock (Fisher and Kerridge 1996; Chapter 4). Studies of native herbivores in the Cerrado savannas have primarily focused on insects (Marquis et al. 2002), reflecting the low diversity and abundance of mammalian herbivores. One study of the mammal community in Brazilian Cerrado documented pampas deer (*Ozotocero bezoarticus*) and brocket deer (*Mazama gouazoubire*) densities of only 0.2 and 3.8 km<sup>-2</sup>, respectively, despite minimal anthropogenic impacts on the study area (Desbiez et al. 2010). The omnivorous collared peccary (*Tayassu tajacu*) and white-lipped peccary (*Tayassu pecari*) occurred at densities of 5.5 and 3.0 km<sup>-2</sup>, respectively (Desbiez et al. 2010). The low abundance of these mammals, and the limited amount of browse in their diets, suggests minimal effects on woody plant dynamics in South American savannas. Comparisons of woody plant traits such as bark thickness and stem height for South American versus African savannas also suggest a primary role of fire in shaping woody plant communities in South American savannas, compared with the combined role of fire and herbivores in African savannas (Dantas and Pausas 2013). In sub-tropical pine savannas of the Florida peninsula of North America, the only mesobrowser is the white-tailed deer (*Odocoileus virginianus*). These deer forage selectively on herbaceous plants of high nutritional quality for much of the year (e.g. Labisky et al. 2003) and typically occur at densities below 10 km<sup>-2</sup>, again suggesting limited potential for feedbacks to woody plant dynamics.

In contrast to the relative lack of mesobrowsers in the Neotropics and Australia, a diverse and abundant community of mesobrowsers occurs in African and Asian savannas. Africa is unrivaled in terms of the current abundance and diversity of large mammalian herbivores. Variation among continents in Pleistocene extinctions rates may have contributed to the depauperate fauna of Australia, North America, and South America, but ecological factors that characterize interior eastern and southern Africa, such as higher elevations, lower precipitation, and greater soil fertility, likely also contribute to Africa's mammalian herbivore diversity and abundance (Owen-Smith 2013). Compared with Africa, less is known about mammalian herbivores in savannas of southern Asia. Early research in Asia often referred to savanna formations as "forest types," even though these communities have a C<sub>4</sub> grass understory combined with a discontinuous woody plant layer (Ratnam et al. 2011; Sankaran and Ratnam 2013). Asian savannas are less extensive than African savannas and studies of herbivore abundance have mostly occurred at sites with greater rainfall (670–2000 mm), but some Asian savannas support abundant cervid and bovid mesobrowsers (Sankaran and Ratnam 2013).

We reviewed mammalian mesobrowser abundance (including mixed-feeding and predominantly browsing species) across African and Asian savannas to provide context for our synthesis of the effects of mesobrowsers on woody plant communities. The value of comparing densities across sites is based on the premise that effects of mesobrowsers on woody plants depend in part on their abundance and the overall proportion of primary productivity they consume, while also recognizing the key role of selective foraging. Research in temperate forests shows mesobrowser effects on plant communities can be disproportionate to the amount of plant biomass consumed due to selective foraging (e.g. Tilghman 1989, McInnes et al. 1992). However, such effects

primarily occur where temperate ungulates are abundant (reviewed by Augustine and McNaughton 1998). Studies of mesobrowser abundance are far more common than the detailed and laborious experiments necessary to document feedback effects on woody plant communities; hence we use our review of mesobrowser abundance to gain initial insight into the role of mesobrowsers in African and Asian savannas.

Mesobrowsers in Africa are generally less abundant than the grazing fauna, comprising ~20% of the total mesoherbivore biomass based on surveys from fixed-wing aircraft (Fritz et al. 2002). However, because aerial surveys from fixed-wing aircraft are strongly biased against the detection of ungulates in woody vegetation, and the magnitude of this bias is rarely measured (Jachmann 2002), analyses of mesobrowser abundance based on more reliable enumeration methodologies are needed. Here, we compare findings from 15 African savanna sites and 11 Asian savanna sites that used ground-based or helicopter surveys to quantify mesobrowser densities (Table 16.1). We also include one estimate from a fixed-wing aerial survey of the central region of Kruger National Park (KNP), because of the extensive literature on mesobrowser and woody plant community ecology at that site. Mean annual precipitation (MAP) for the African sites ranges from 400 to 1100 mm, which represents the range of MAP within the savanna biome on the continent (Sankaran et al. 2005). We did not find mesobrowser density estimates for any Asian savannas receiving <670 mm MAP. We include Asian sites with up to 2000 mm MAP, which includes sites that transition from more open woody cover (e.g. dry thorn or dry deciduous forest) to less open woody cover (e.g. moist deciduous forest). To relate mesobrowser density to effects on woody plant communities (see below), we report density estimates both from a large spatial extent and from the immediate vicinity of exclosure studies at the Chobe and Kruger sites (Moe et al. 2009; Scogings et al. 2012). For the Laikipia and Hluhluwe-iMfolozi sites, we note that density estimates are equivalent at the scale of the survey area reported in Table 16.1 and the scale of the exclosure studies discussed later.

In African savannas, the most widely distributed mesobrowsers are impala (*Aepyceros melampus*), greater kudu (*Tragelaphus strepsiceros*), and eland (*Taurotragus oryx*; Table 16.2). These species represent a body size gradient, with the smallest (impala) often most abundant, whereas greater kudu and eland typically occur at far lower numerical densities. Nyala (*Tragelaphus angasii*) are intermediate in body size between impala and greater kudu and contribute significantly to mesobrowser biomass in some mesic savannas of south-eastern Africa (e.g. Lagendijk et al. 2011; O’Kane et al. 2012). The contribution of mesobrowsers smaller than impala varies and depends on the species present (Table 16.2). Steenbok (*Raphicerus campestris*) and gray duiker (*Sylvicapra grimmia*) are relatively widespread across eastern and southern Africa, but occur at consistently low densities (Table 16.2). In contrast, dik-dik (*Madoqua kirkii* and *M. guntherii*) can occur at densities  $>50 \text{ km}^{-2}$  in some eastern and south-western African savannas (e.g. Amubode and Boshe 1990; Komers and Brotherton 1997; Augustine 2010), but are absent from much of southern Africa. Pure browsers only rarely attain biomass densities on the same order of magnitude as impala. Of note are dik-dik (Laikipia), greater kudu (Ithala, Tuli, Loskop Dam, and Hwange open woodland), and eland (Massai Mara and Tuli; Table 16.2).

In Asian savannas, mesobrowsers are more abundant and diverse compared with the Neotropics and Australia, and in many cases occur at densities similar to, or greater than, African savannas (Table 16.3). Chital (*Axis axis*), sambar (*Rusa unicolor*), and nilgai

**Table 16.1** African and Asian savannas where mesobrowser densities have been measured using ground-based methods or helicopter counts.

Country	Site	Method	MAP (mm)	Survey area (km <sup>2</sup> )	Vegetation	Citation
<b>Africa</b>						
Botswana	Chobe (A)	Ground transects	700	400	<i>Baikiaa</i> woodland; <i>Capparis/Combretum</i> riverine shrubland	Skarpe et al. (2014b)
Botswana	Chobe (B)	Local estimate	700	1.5	<i>Capparis/Combretum</i> riverine shrubland	Moe et al. (2009)
Kenya	Tsavo South-east	Ground transects	375	2800	Thinned <i>Commiphora</i> savanna	Leuthold and Leuthold (1976)
Kenya	Laikipia	Ground transects	515	82	<i>Acacia</i> bushland	Augustine (2010)
Kenya	Nakuru	Ground mapping censuses	870	166	Diverse	Ogutu et al. (2012)
Kenya	Koyaki	Ground mapping censuses	1010	931	<i>Acacia/Terminalia</i> open savanna	Bhola et al. (2012)
Kenya	Massai Mara	Ground mapping censuses	1010	1530	<i>Acacia/Terminalia</i> open savanna	Bhola et al. (2012)
South Africa	Tuli	Ground transects	400	600	<i>Acacia/Boscia/Salvadora</i> savanna	Walker et al. (1987)
South Africa	Klaserie	Ground transects	475	600	<i>Acacia</i> savanna and broad-leaved savanna	Walker et al. (1987)
South Africa	Kruger (A)	Fixed-wing aerial; 50% detection correction	625	5000	<i>Acacia</i> savanna and <i>Combretum</i> woodland	Walker et al. (1987)
South Africa	Kruger (B)	Local estimate	550	1.6	<i>Dichrostachys/Acacia</i> savanna	Scogings et al. (2012)
South Africa	Hluhluwe-iMfolozi (A)	Ground transects	600–720	900	Diverse	Staver et al. (2009)
South Africa	Hluhluwe-iMfolozi (B)	Ground transects	635	108	Open <i>Acacia</i> and closed <i>Spirostachys</i> woodland	O’Kane et al. (2012)
South Africa	Loskop Dam	Helicopter counts	655	85	<i>Combretum/Acacia/Terminalia</i> savanna	Reilly 2002
South Africa	Phinda	Helicopter count	350–1100	180	Diverse	Legendijk et al. (2012)

(Continued)

Table 16.1 (Continued)

Country	Site	Method	MAP (mm)	Survey area (km <sup>2</sup> )	Vegetation	Citation
South Africa	Ithala	Ground-based and aerial census	781	296	Mixed <i>Acacia</i> and other savannas	Gordijn et al. (2012)
Zimbabwe	Hwange East	Ground transects	600	2800	Open <i>Baikaia</i> and other woodland	Chamaille-Jammes (2009)
Zimbabwe	Hwange West	Ground transects	600	2000	<i>Colophospermum</i> savanna	Chamaille-Jammes (2009)
<b>Asia</b>						
India	Gir Forest	Ground transects	670	1008	Dry thorn and dry deciduous forest	Khan et al. (1996)
India	Ranthambore (A)	Ground transects	800	260	Dry thorn and dry deciduous forest	Karanth and Nichols (2000)
India	Ranthambore (B)	Ground transects	800	34	Dry thorn and dry deciduous forest	Bagchi et al. (2004)
India	Pilibhit	Ground transects	800	420	Sal savanna or forest	Bista (2011)
India	BRTWLS <sup>a</sup>	Ground transects	645–1105	610	Dry deciduous, moist deciduous, scrub, and evergreen forest	Kumara et al. (2012)
India	Panna	Ground transects	1075	103	Dry deciduous forest	Gopal et al. 2010
India	Pench (A)	Ground transects	1090	150	Dry and moist deciduous forest	Karanth and Nichols (2000)
India	Pench (B)	Ground transects	1090	61	Dry and moist deciduous forest	Biswas and Sankar (2002)
India	KMTR <sup>b</sup>	Ground transects	1200	60	Savanna grassland and dry deciduous forest	Sankaran (2001)
India	Bandipur	Ground transects	705–1980	270	Dry and moist deciduous forest	Karanth and Nichols (2000)
India	Rajiv Gandhi (Nagarahole)	Ground transects	875–2270	220	Dry and moist deciduous forest	Karanth and Sunquist (1992), and Karanth and Nichols (2000)
India	Mudumalai	Ground transects	1190–2750	107	Dry thorn, dry deciduous and moist deciduous forest	Ramesh et al. (2012), and Ramesh (2010)
India	Kanha	Ground transects	1355	290	Moist deciduous forest	Karanth and Nichols (2000)
Nepal	Royal Karnali-Bardia	Platform counts; ground transects	1825	12	Moist deciduous forest; sal savanna or forest	Dinerstein (1980)

For sites with two independent herbivores density estimates conducted at differing spatial scales, estimates at the largest scale are listed first (A) followed by the second estimate at the smaller scale (B), where (B) is nested within (A).

<sup>a</sup> Billigiri Rangaswamy Temple Wildlife Sanctuary.

<sup>b</sup> Kalakad-Mundanthurai Tiger Reserve.

**Table 16.2** Mesobrowser densities for 15 savanna sites in eastern and southern Africa (see Table 16.1 for sources and site descriptions).

	Mixed-feeders				Browsers			
	Impala (40)	Grant's Gazelle (40)	Shoats (18)	Dik-dik (5)	Duiker and Steenbok (10)	Gerenuk (25)	Lesser Kudu (70)	Eland (340)
<b>East Africa</b>								
Laikipia	20.3	0.0	0.4	97	0.5	0.0	0.0	0.4
Nakuru	18.1	1.7	0	0	0.0	0.0	0.0	0.4
Koyaki	10.7	1.8	46.6	0	0.0	0.0	0.0	0.2
Massai Mara	5.3	2.1	14.7	0	0.0	0.0	0.0	1.2
Tsavo South-east	1.1	0.5	0	0	0.0	0.6	0.2	0.1
<b>Southern Africa</b>	Impala (40)	Nyala (73)			Duiker and Steenbok (10)	Greater Kudu (136)	Eland (340)	
Chobe (A)	10.2	0			0.1	1.1	0.2	
Chobe (B)	50.0	0			0.0	NR	NR	
Loskop Dam	3.7	0			0.0	3.0	0.0	
Phinda GR	9.4	9.7			0.0	1.0	0.0	
Ithala GR	9.5	0.9			0.0	2.6	0.3	
Tuli GR	27.0	0			0.0	3.2	1.3	
Klaserie GR	30.1	0			0.0	0.8	0.0	
Kruger (A)	17.4	0			0.0	1.3	0.0	
Kruger (B)	23.6	0			0.0	NR	0.0	
Hluhluwe- iMfolozi (A)	22.2	2.5			0.0	1.1	0.0	
Hluhluwe- iMfolozi (B)	36.2	2.4			0.0	0.6	0.0	
Hwange Open	1.3	0.00			2.8	2.0	0.0	
Hwange Mopane	9.6	0.00			0.2	1.3	0.0	

Units are individuals km<sup>-2</sup> and numbers in parentheses below each species are mean body mass in kg, based on sources in Table 16.1 NR = species present but density not reported.

(*Boselaphus tragocamelus*) are the most widespread and abundant mesobrowsers in Indian savannas (Table 16.3) and represent a body size gradient similar to that of impala, greater kudu, and eland in African savannas. Smaller ungulates include the chinkara (Indian gazelle, *Gazella bennettii*) in semi-arid areas, and the chousingha (four-horned antelope, *Tetracerus quadricornis*) and common muntjac (barking deer, *Muntiacus muntjak*) in mesic woody communities. These species occur at relatively low densities

**Table 16.3** Mesobrowser densities for 10 savanna sites in southern Asia (see Table 16.1 for sources and site descriptions).

Country	Site name	Mixed-feeders				Browsers	
		Chital (45)	Sambar (135)	Nilgai (180)	Chinkara (23)	Chousingha (21)	Muntjac (21)
India	Gir Forest	50.8	2.1	0.6	2.2	0.4	0.0
India	Ranthambore (A)	38.4	10.7	6.6	1.3	0.0	0.0
India	Ranthambore (B)	31.0	17.1	11.4	5.6	0.0	0.0
India	Pilibhit	22.4	0.0	12.0	0.0	0.0	0.0
India	BRTWLS	14.0	6.0	0.0	0.0	2.4	3.7
India	Panna	16.3	11.9	16.1	NR	NR	0.0
India	Pench Tiger Reserve (A)	51.3	9.6	0.7	0.0	0.7	0.0
India	Pench Tiger Reserve (B)	80.8	6.1	0.4	0.0	0.3	0.0
India	KMTR	1.9	2.8	0.0	0.0	0.0	0.0
India	Bandipur	20.1	5.6	0.0	0.0	1.1	0.7
India	Rajiv Gandhi (Nagarahole)	44.4	4.9	0.0	0.0	0.0	5.1
India	Mudumalai	43.8	4.9	0.0	0.0	0.0	1.2
India	Kanha	49.7	1.5	0.0	0.0	0.0	0.6
Nepal	Royal Karnali-Bardia	31.8	0.0	5.0	0.0	0.0	1.7

Units are individuals km<sup>-2</sup> and numbers in parentheses below each species name are mean body mass in kg, based on sources in Table 16.1.

(e.g. similar to steenbok and duiker in Africa; Tables 16.2 and 16.3). No small (<20 kg) Asian ungulates are known to attain densities comparable with dik-dik in Africa.

Finally, we acknowledge that domestic mesobrowsers, primarily goats and camels, are an important contemporary component of tropical savannas worldwide. However, we do not address effects of domestic mesobrowsers on woody plant communities in this chapter due to a surprising lack of accurate estimates of goat and camel densities, as well as a lack of long-term, experimental studies of their impacts on woody plant communities (but see Hester et al. 2006). Accurate estimates of goat densities are particularly difficult to obtain due to uncertainty in the area over which a given herd forages, and lumping of sheep with goats (shoats) in many surveys. Long-term, experimental studies linking goat densities with impacts on woody plant communities are clearly needed.

## 16.3 Mesobrowser Diets in Savannas

Diet composition of mammalian herbivores varies dramatically among species, within species, among seasons, and even locally depending upon the plant species available. Quantifying variation in herbivore diets is logistically challenging, but also central to understanding and predicting long-term herbivore effects on savannas. We reviewed diet composition and foraging selectivity of mesobrowsers that typically consume <80% grasses annually in African and Asian savannas (species in Tables 16.2 and 16.3), focusing on variation among and within species in the relative consumption of grasses versus woody plants. For Africa, we focus on studies that measured  $^{13}\text{C}$  in the feces because of the wide geographical scope of such studies in Africa, and because it yields findings comparable with more labor-intensive observational studies (Codron et al. 2007). For Asia, we review observational studies because we found only one study that used fecal  $^{13}\text{C}$  analysis.

Of the African mesobrowsers, impala, nyala, and Grant's gazelle (*Nanger granti*) consistently consume grasses during wet seasons followed by a shift to woody species as grass digestibility declines during senescence. For impala,  $\text{C}_4$  grasses comprise roughly half the annual diet (Table 16.4). In comparison, nyala and Grant's gazelles consume less grass (20–30% of annual diet), but may consume a greater mixture of forbs and woody plants. Although the grass:browse ratio of these species' diets will vary with grass:tree balance and plant species composition, impala consistently consume 36–60% grasses annually across a wide range of conditions (Cerling et al. 2003; Sponheimer et al. 2003; Codron et al. 2007; Augustine 2010; Miranda et al. 2014; Table 16.4). Species consuming nearly pure browse diets encompass a wide range of body sizes, including dik-dik, common duiker, gerenuk, lesser kudu, greater kudu, and eland (Table 16.4).

In Asian savannas, diet selection studies for the six most common mesobrowsers (chital, sambar, nilgai, chinkara, chousingha, muntjac) are sparse, and findings vary within a given species. Chital may consume >90% grass during wet seasons (Schaller 1967; Dinerstein 1979). Some chital populations are strongly affected by competition with cattle for grass forage (Khan et al. 1996; Madhusudan 2003), suggesting substantial dependence of chital on grass intake. However, other studies report considerably less wet season grass consumption (30–70%) and a substantial increase in browse consumption during wet to dry season transitions and dry seasons (Bagchi 2003; Ahrestani et al. 2012).

**Table 16.4** Relative amounts of grass versus browse in the diets of 10 African mesobrowser species, based on studies of  $^{13}\text{C}$  in fecal samples.

		% C4 in diet				Mean	% Browse intake weighting
		Regional-scale studies		Site-scale studies			
		East Africa	South Africa	Laikipia	KNP		
Impala	<i>Aepyceros melampus</i>	52	51	36	60	50	50
Grant's gazelle	<i>Gazella grantii</i>	22	—	—	—	22	80
Nyala	<i>Tragelaphus angasii</i>	—	33	—	23	28	70
Dik-dik	<i>Madoqua</i> spp.	0	—	0	—	0	100
Steenbok	<i>Raphicerus campestris</i>	18	10	—	7	12	90
Common duiker	<i>Sylvicapra grimmia</i>	0	2	—	15	6	90
Gerenuk	<i>Litocranius walleri</i>	2	—	—	—	2	100
Lesser kudu	<i>Tragelaphus imberbis</i>	0	—	—	—	0	100
Greater kudu	<i>Tragelaphus strepsiceros</i>	4	4	—	7	5	100
Eland	<i>Taurotragus oryx</i>	18	8	8	3	9	90

Sources for East Africa, South Africa, Laikipia, and Kruger National Park (KNP) are Cerling et al. (2003), Sponheimer et al. (2003), Augustine (2010), and Codron et al. (2007), respectively. Percentage browse in the diet was calculated as  $(100 - \% \text{C}_4 \text{ in the diet, rounded to the nearest } 10\%)$ , and was used in combination with data in Table 16.2 to estimate the metabolic biomass density of that portion of the total mesoherbivore community consuming browse (Table 16.5).

Browse consumption by chital can also be highly selective. Dinerstein (1979) reported that chital consumed 31 woody species in a Nepalese savanna, of which 15 were consumed to a greater degree than expected based on availability. Thus, although chital appear to consume more grass than African mixed-feeders such as impala, the high densities they achieve in some savannas (Table 16.3), combined with selective feeding on woody plants during dry seasons and wet–dry transitions, could have significant implications for woody plant communities.

Sambar, nilgai, and chinkara are also mixed-feeders, but consume greater amounts of browse compared with chital (Solanki and Naik 1998; Ahrestani et al. 2012; Bhat et al. 2012). Analyses of fecal  $^{13}\text{C}$  for sambar in Bandipur and Mudumalai Tiger Reserves indicate that grasses comprise only 10–20% of the annual diet (depending upon assumptions for  $^{13}\text{C}$  in  $\text{C}_4$  vs  $\text{C}_3$  plant tissues, which have not been measured at this site; Ahrestani et al. 2012). Other studies suggest a grass: browse intake ratio for sambar in the order of 50:50 (Bagchi 2003), or that sambar principally consume browse (Ismail and Jiwan 2015). When feeding in a grass-dominated study area, nilgai and chinkara consumed intermediate amounts of grass (29–44%; Solanki and Naik 1998). In another savanna, nilgai consumed 42% grass and 23% woody foliage, while 36% of intake consisted of fallen flowers, fruits, and leaves (Bhat et al. 2012). Improved knowledge of how

browse intake is partitioned between fallen fruits or leaves versus foliage removed directly from woody plants will likely be important in assessing impacts on woody plants. Although consumption of fallen material will not directly impact woody plant growth, it can help sustain high densities of mesobrowser populations, which in turn impact those woody plants from which they directly remove foliage. Bhat et al. (2012) and Ismail and Jiwan (2015) also noted strong selectivity by nilgai and sambar feeding on woody plants.

Chousingha and Indian muntjac are small, similarly-sized browsing ungulates that differ in fine-grained habitat selection where they co-occur (Pokharel et al. 2015). Measures of grass intake for chousingha vary from <10% (Solanki and Naik 1998; Sharma et al. 2009) to 29% (Baskaran et al. 2011). As with the mixed-feeding ungulates, browse consumption may include variable amounts of fallen leaves, fruits, or flowers, versus foliage consumed directly from woody plants (Sharma et al. 2009; Baskaran et al. 2011).

To compare mesobrowser biomass density across African and Asian savannas in a manner that accounts for variation in mixed-feeder versus browser abundance, we first calculated total biomass density and metabolic biomass density of each species as the product of their density (individuals  $\text{km}^{-2}$ ) and either biomass (mean kg per individual as reported in Tables 16.2 and 16.3) or metabolic biomass (mean kg per individual raised to the 0.75 power). We then calculated total browser biomass and total browser metabolic biomass by using the browse intake weighting values for African species shown in Table 16.4. For Asian species, the browse intake weighting is more speculative and based on the above review, and likely varies among species across their range. We present calculations of mesobrowser metabolic biomass multiplied by browse intake estimates of 20, 60, 60, 50, 90, and 90% for chital, sambar, nilgai, chinkara, chousingha, and muntjac, respectively (Table 16.5).

Several notable patterns emerged from our comparison of mesobrowser abundance across sites and continents (Table 16.5). First, abundance varied by an order of magnitude among African sites, from 35  $\text{kg km}^{-2}$  in Tsavo to 517  $\text{kg km}^{-2}$  in Laikipia. African sites with >300  $\text{kg km}^{-2}$  ( $n = 4$ ) are characterized by either moderate densities of impala combined with high densities of one pure browser (Laikipia with dik-dik; Tuli with greater kudu), or high densities of impala (Chobe and Hluhluwe-iMfolozi). Relative to the African savannas, Asian savannas were characterized by greater MAP, greater mesobrowser biomass (range: 214–880  $\text{kg km}^{-2}$ ), and a general lack of pure browsers (Table 16.5). Even assuming that chital consume only 20% browse annually, chital contributed substantially to the weighted browser metabolic biomass. The five Asian sites with browser metabolic biomass >300  $\text{kg km}^{-2}$  (Ranthambore, Panna, Pench, Pilibhit, and Rajiv Gandhi) also contained high densities of sambar or nilgai (Tables 16.3 and 16.5).

## 16.4 Mesobrowser Effects on Woody Plant Communities

In contrast to the extensive literature concerning elephant effects on savanna vegetation, less attention has been focused on the effects of mesobrowsers. Numerous methodological challenges likely contribute to this knowledge gap. These include (i) the long time scales required to detect browser effects on plant growth, reproduction, and mortality; (ii) costly methods involved in simply measuring browse production and consumption rates; and

**Table 16.5** Comparison of estimated metabolic biomass of mesobrowsers in African and Asian savannas.

Country	Site	Metabolic biomass (kg km <sup>-2</sup> )			Sum of (metabolic biomass × % browse intake for each species)
		Mixed-feeders	Browsers	Total	
<b>Africa</b>					
Kenya	Tsavo South-east	26	20	46	35
Zimbabwe	Hwange Open	20	95	115	104
Kenya	Koyaki <sup>a</sup>	199	14	213	121
Zimbabwe	Hwange Mopane	152	53	204	128
Botswana	Chobe (A)	162	60	222	140
South Africa	Loskop Dam	59	121	180	151
Kenya	Massai Mara <sup>a</sup>	118	94	212	154
South Africa	Kruger (B)	375	0	375	188
South Africa	Kruger (A)	276	52	329	190
Kenya	Nakuru	315	32	347	194
South Africa	Ithala GR	172	125	297	213
South Africa	Hluhluwe-iMfolozi (A)	416	45	461	266
South Africa	Klaserie GR	479	34	513	273
South Africa	Phinda GR	392	40	432	284
South Africa	Hluhluwe-iMfolozi (B)	635	25	660	354
Botswana	Chobe (B)	795	0	795	398
South Africa	Tuli GR	429	234	664	438
Kenya	Laikipia	323	359	682	517
<b>Asia</b>					
India	KMTR <sup>b</sup>	144	0	144	73
India	Kanha	923	6	929	214
India	Bandipur	571	18	589	219
India	BRTWLS <sup>c</sup>	481	60	541	246
India	Gir Forest	1017	4	1021	259
Nepal	Royal Karnali-Bardia	798	17	815	273
India	Mudumalai	955	12	967	279
India	Rajiv Gandhi	963	50	1013	314
India	Pilibhit	979	0	979	432
India	Pench (A)	1306	7	1313	433
India	Pench (B)	1665	3	1668	441
India	Ranthambore (A)	1429	0	1429	589

Table 16.5 (Continued)

Country	Site	Metabolic biomass (kg km <sup>-2</sup> )			Sum of (metabolic biomass × % browse intake for each species)
		Mixed-feeders	Browsers	Total	
India	Panna	1546	0	1546	814
India	Ranthambore (B)	1835	0	1835	880

See Table 16.1 for the methods used to estimate herbivore densities at each site. The first three columns with numerical values show the sum of metabolic biomass for mixed-feeding species, browsing species, and all species, respectively, for the species listed in Tables 16.2 and 16.3. The last column shows the sum of (metabolic biomass × estimated % browse in the diet) across all species occurring at a given site. For estimates of % browse in the diet, see Table 16.4 for African species and the text for Asian species.

<sup>a</sup> Excluding sheep and goats.

<sup>b</sup> Kalakad-Mundanthurai Tiger Reserve.

<sup>c</sup> Biligiri Rangaswamy Temple Wildlife Sanctuary.

(iii) the lack of cost effective means to examine root growth and below-ground storage in woody plants. Much of our knowledge of the influence of climate, soils, and fire on savannas has been derived from comparative studies across savannas (Sankaran et al. 2008; Lehmann et al. 2014). This approach has been challenging with respect to mesobrowsers because accurate and comparable measurements of variation in mesobrowser abundance across landscapes or among study sites are typically lacking. In addition, the effects of mesobrowsers within a given savanna site are often dependent on multiple factors associated with the local setting, including the landscape context, which are difficult to quantify as covariates for comparative analyses.

Recognition that (i) mesobrowsers forage in a selective manner and (ii) woody plants in savannas display a wide variety of physical and chemical traits that deter mammalian herbivores, suggests mesobrowsers likely have feedback effects on the structure, composition, and growth rate of woody plant communities (Chapter 15). Yet, quantifying the nature and strength of these effects requires long-term research addressing the issue from both plant and animal perspectives. Our ability to compare such effects across different savannas, and thereby elucidate key drivers of mesobrowser effects on savannas, hinges on comparisons of (i) mesobrowser abundance and the controls over that abundance within a given system; (ii) seasonal variation among mesobrowsers in their use of woody vs herbaceous forage; (iii) selectivity of foraging by different mesobrowsers; (iv) climatic and edaphic controls on woody plant growth rates; and (v) responses of woody plants to manipulations of mesobrowser abundance (e.g. removal via exclosures) at scales from individual twigs to the landscape. Obtaining this breadth of understanding from multiple savanna ecosystems in a manner that is quantitatively comparable is a clearly daunting task. Measures of (v) are further complicated by our desire to separate the effects of mesobrowsers from those of megabrowsers.

We begin to address this challenge by examining four case studies of African savannas where we can link measurements of mesobrowser abundance (Tables 16.2–16.5) with exclosure experiments quantifying plant community response to mesobrowser removal as well as studies of mesobrowser foraging behavior. The depth and intensity of work on

each of the five topics varies among the case studies, and quantitative measurements are too variable in units and limited in accuracy and replication to permit formal meta-analysis. Instead, we outline how mesobrowser abundance, selective foraging in time and space, functional traits of the woody plants, and climatic and edaphic controls on plant growth contribute to our ability to predict the nature and strength of mesobrowser effects on woody plants. We supplement these case studies with four additional vignettes from long-term studies that documented changes in woody plant communities likely related to the influence of mesobrowsers, and two vignettes based on studies of localized high densities of a single mesobrowser species.

#### 16.4.1 Hluhluwe-iMfolozi Park, South Africa

Hluhluwe-iMfolozi Park (HiP) is a 900-km<sup>2</sup> fenced preserve in the KwaZulu-Natal province of South Africa. Plant communities are varied, but mesobrowser studies focus on plant communities dominated by *Acacia nilotica*, *A. karroo*, and *Dichrostachys cinerea*, or *Euclea divinorum* in the Hluhluwe portion and communities dominated by *A. tortilis*, *A. nigrescens*, or *Spirostachys africanus* in the iMfolozi portion. Principal mesobrowsers are impala, kudu, and nyala (Table 16.2), while megabrowsers are elephant, giraffe, and black rhino (*Diceros bicornis*). Two complementary approaches have been used to provide a particularly robust picture of how plant and animal traits shape the plant–herbivore interaction.

First, O’Kane and colleagues quantified habitat and plant species selection by the primary mesobrowsers (O’Kane et al. 2011, 2013) and demonstrated that spatial variation in woody seedling recruitment varies with impala densities across the landscape (O’Kane et al. 2012). Findings were used to parameterize a browse–browser model of the relative influence of impala and elephant on woody plant functional groups, where functional groups were defined based on woody plant recruitment, growth, and utilization rates (O’Kane et al. 2014). A key finding was the strong, synergistic effect of impala and elephant on woodland dynamics, such that removal of either herbivore could dramatically increase woodland development. Model predictions over a 100-year time frame for low elephant densities without impala versus low elephant densities with medium impala densities indicated large (>95%) declines in the densities of *Ziziphus* and *Spirostachys* species, moderate (35–75%) declines in densities of *Acacia*, *Dichrostachys*, and *Maytenus* (= *Gymnosporia*) species, and no changes in densities of *Euclea* and *Sclerocarya* species (O’Kane et al. 2014).

A second approach used enclosure experiments to quantify browser effects at HiP, including interactions with fire intensity, by employing enclosures that removed both megabrowsers and mesobrowsers, or selectively removed megabrowsers, but not mesobrowsers (Staver et al. 2009; Staver and Bond 2014). Experimental sites were distributed across a MAP gradient of 650–720 mm, and encompassed savannas containing *Acacia* spp., *Maytenus* spp., *D. cinerea*, and *E. divinorum*. Browsers largely prevented woody plant recruitment from below 2 m to larger size classes, primarily due to the impact of mesobrowsers. Model projections based on enclosure results indicated that over a 200-year time frame, the combination of browsing by mesobrowsers (impala and nyala) and megabrowsers (elephant, giraffe, and black rhino) would eliminate *Acacia gerrardii* and *A. nigrescens* from the canopy layer, reduce the density of *A. karroo* and *Maytenus heterophylla* by >90%, and have no effect on, or enhance, the abundance of *D. cinerea* and

*E. divinorum*, as compared with the woody community projected under a scenario of browsing by black rhino only. These predictions did not separate the effects of mesobrowsers from those of elephant and giraffe on woody plant species composition (Staver et al. 2009). However, exclosure results indicated that changes in total woody plant density were due primarily to mesobrowsers rather than elephants and giraffe (Staver and Bond 2014).

O’Kane et al. (2014) also predicted similar declines in *Acacia* spp. and *Maytenus* spp. with increasing density of impala when elephant remain at a constant, moderate density. The two modeling approaches diverged in projections for the plant strategy of high growth and recruitment rates combined with high palatability (represented by *D. cinerea*, which has higher recruitment rate than *Acacia* spp.), with either elimination by mesobrowsers (O’Kane et al. 2014), or enhancement by mesobrowsers (Staver et al. 2009), suggested. In reality, *D. cinerea* has been increasing in HiP and O’Kane et al. (2014) noted that the growth rate estimate used in their model (derived from the broader literature) was likely inappropriately low for this species. Sensitivity of model predictions to plant growth rate estimates highlights how mesobrowser effects (and outcomes for considerably different plant defense strategies) are still contingent on climatic and edaphic controls on plant growth rate (Chapter 12, this volume).

Both field and modeling results presented by Staver et al. (2009) suggest woody plant persistence and species composition depend on spatiotemporal variation in mesobrowser abundance. This conclusion is consistent with the correlation between woody plant recruitment pulses and spatiotemporal variation in impala abundance (O’Kane et al. 2012; Staver and Bond 2014), and independent model projections based on woody plant demography and simulated responses to browsing (O’Kane et al. 2014). Collectively, these studies demonstrate that mesobrowsers can regulate the balance between woody plants and grasses, and act as a filter that shifts the composition of woody communities toward increased dominance by certain broad-leaved species with low to moderate growth and recruitment rates that are avoided by mesobrowsers (e.g. *Euclea* spp.). The avoided broad-leaved species are typically well endowed with secondary metabolites, especially phenolics (Scogings et al. 2014). Whether or not other woody species with high growth rates (e.g. *D. cinerea*) can also persist through the browse filter and potentially increase with moderate or high mesobrowser densities depends upon factors controlling woody plant growth rates and interactions with the fire regime (Staver and Bond 2014; O’Kane et al. 2014).

#### 16.4.2 Central Laikipia, Kenya

Savanna dominated by *Acacia mellifera*, *A. etbaica*, and *A. brevispica* occurs on sandy loam soils dissected by near-permanent rivers and associated ephemeral drainages across the central region of Laikipia County, Kenya, where MAP ranges from 450 to 550 mm. Dominant mesobrowsers are dik-dik, impala, and eland (Table 16.2), which coexist with elephant and giraffe. The high density of diminutive dik-dik (~5 kg; browsing height typically less than 0.75 m) is a notable difference from southern African savannas, which generally lack significant densities of browsers of similar size. Impala primarily consume grass in wet seasons and browse in dry seasons, while dik-dik and eland are year-round browsers (Augustine 2010). Analysis of herbivore diets based on fecal DNA showed that all dominant *Acacia* species (with varying investment in spines)

occur in  $\geq 63\%$  of impala and dik-dik fecal samples, and even *Grewia* spp. (rare outside exclosures) occur in  $\geq 22\%$  of the samples from both impala and dik-dik (Kartzinel et al. 2015). Measurements of *A. mellifera* and *A. etbaica* twigs at varying heights inside vs outside exclosures showed both species experience substantial reductions in leaf number and mass for twigs within the browsing height of dik-dik, but not for twigs above that height (Augustine and McNaughton 2004). Consumption of twigs below 1 m height by elephants was rare ( $< 1\%$  annually), so reductions in leaf biomass, and associated suppression of twig growth rates, could be attributed to mesobrowsers, particularly dik-dik. Furthermore, *A. mellifera* (larger leaves, recurved spines) experienced greater reductions in leaf biomass on twigs within dik-dik reach compared with *A. etbaica* (smaller leaves, both recurved spines and long, straight spines). Whether browsing of *A. etbaica* is reduced by the small leaves, straight spines, the combination of recurved and straight spines, or unknown secondary metabolites, is unclear. Broad-leaved, palatable woody species were rare, consisting mainly of *Grewia tenax* and *Rhus natalensis* (= *Searsia natalensis*), which were either intensively defoliated or avoided herbivory by growing inside of “cages” created by *Acacia* species.

Within 3 years, browser exclusion resulted in a 6-fold increase in woody plant recruitment into size classes above dik-dik browsing height (145.8 woody plants  $\text{ha}^{-1} \text{year}^{-1}$  inside versus 25.8  $\text{ha}^{-1} \text{year}^{-1}$  outside exclosures), but no change in recruitment to size classes above impala or eland browsing height (Augustine and McNaughton 2004). After 10 years, these dramatic differences in transition rates inside vs outside exclosures persisted, but additional patterns emerged. First, mortality rates of species other than *A. etbaica* were elevated in the presence of browsers (not differentiated between meso- vs megabrowser effects). Second, browser effects on both recruitment and mortality rates of *A. etbaica* diverged from the remainder of the woody plant community, such that size class transition probabilities predict long-term *A. etbaica* persistence or increases under the current browsing regime, while most other species decline (Sankaran et al. 2013). The shift in species composition and suppression of total woody cover are attributable to the combination of mesobrowsers and elephants, but mesobrowsers exert the strongest influence on woody plant density and contribute substantially to the compositional shift. In contrast, elephant browsing mainly affects woody plant biomass and size class distributions, but not woody plant density (Augustine and McNaughton 2004; Sankaran et al. 2013).

During the course of these studies (1999–2009), mesobrowser biomass density was exceptional, even by African standards, with dik-dik densities averaging  $139 \text{ km}^{-2}$  (Augustine 2010). Subsequent recolonization by African wild dogs (*Lycaon pictus*) reduced dik-dik abundance approximately 30% (Ford et al. 2015). Additional exclosures constructed after wild dog recolonization show that even at their reduced densities ( $\sim 97 \text{ km}^{-2}$ ; Table 16.2), dik-dik continue to suppress seedling-to-sapling recruitment rates of dominant *Acacia* species to the same degree as prior to wild dog recolonization (Ford et al. 2015). Furthermore, differences in impala and *Acacia* distribution between uplands and drainages suggest that, in some portions of the landscape, impala may constrain the large-leaved and minimally armed *A. brevispica* to more fertile and densely wooded drainages that impala avoid due to predation risk (Ford et al. 2014).

Collectively, these studies show that mesobrowsers affect woody plants in ways that are distinct from elephants and fundamentally alter the structure and composition of the woody layer. Most notably, (i) broad-leaved, palatable species rarely grow through

the browser filter; (ii) the only spinescent species with sustainable recruitment rates (*A. etbaica*) has a high level of investment in spines relative to other *Acacia* species (i.e. not all spiny species persist); but (iii) unpalatable broad-leaved species do not dominate the community in the presence of browsers (Sankaran et al. 2013). These latter two outcomes could perhaps be related to tradeoffs between growth rate constraints from edaphic factors and investments in secondary metabolites, as broad-leaved, unpalatable species with long-lived leaves (e.g. *Croton dichogamous* and *E. divinorum*) still do not increase relative to *A. etbaica*, despite the fact that the latter is consumed by browsers and the former are not.

### 16.4.3 Chobe National Park, Botswana

Along the Chobe River in Chobe National Park, northern Botswana, elephant browsing has fragmented the canopy of a formerly well-developed belt of mixed gallery woodlands, with openings replaced by shrubs and thickets (Mosugelo et al. 2002; Rutina 2004; Skarpe et al. 2014b). Lack of subsequent tree regeneration in these openings called into question the influence of elephants versus mesobrowsers, particularly given that impala have reached high localized densities ( $50 \text{ km}^{-2}$ , Moe et al. 2009) along the riverfront. Unlike the previous two examples, the only abundant mesobrowser here is impala, along with smaller numbers of kudu (Table 16.2). Despite some diet overlap, elephant browse on a wider range of plant heights than impala, and elephants and impala differ in the dominant woody species in their diets (*Combretum elaeagnoides* for elephant, *Capparis tomentosa* and *Combretum mossambicense* for impala), suggesting they could have different effects on woody composition (Makhabu 2005; Moe et al. 2014).

Exclosure experiments with transplanted seedlings of four species in the riverine woodlands and shrublands showed that impala browsing, which increased markedly at the wet to dry season transition, was the primary cause of mortality for the three most palatable species (Moe et al. 2009). Furthermore, impala browsing still induced moderate mortality for a less palatable, broad-leaved species (Moe et al. 2009). Natural seedling regeneration also increased 6-fold inside exclosures, while seedling mortality outside exclosures was positively correlated with local variation in impala density (Moe et al. 2009). In this case, we see clear experimental evidence that even a single mixed-feeding species can achieve sufficiently high densities to suppress regeneration of both unarmed species (e.g. *Garcinia livingstonei*) and spinescent species (e.g. *Faidherbia albida* and *C. mossambicense*), while certain unarmed, broad-leaved species (e.g. *Croton megalobotrys*) can persist through the browser filter, presumably because of secondary metabolites. Of particular interest in this system is the relationship between impala and *C. mossambicense*. This woody species typically only reaches 3 m in height in free-standing form, but may reach 5–6 m by growing into, or on the support structures of, other woody species (Coates-Palgrave 2002). Although intense browsing causes significant sapling mortality for *C. mossambicense* (Moe et al. 2009), and impala consume more *C. mossambicense* than any other plant species during the wet season (Makhabu 2005), it is still increasing in absolute and relative abundance in the riverine savanna, particularly in sites with high impala density (Moe et al. 2014). This outcome has parallels to the dynamics of *D. cinerea* in HiP, and highlights how palatability and herbivore density alone cannot necessarily predict interactions between mesobrowsers and the woody plant community. Factors controlling seedling establishment and growth rate

can be important in allowing palatable species to persist or increase in the face of substantial defoliation rates (Moe et al. 2014).

Studies in the Chobe riverine savanna also highlight the influence of landscape features on plant–herbivore interactions. In this case, the adjacent perennial water source, and the ability of herbivores to disperse across a broad landscape in wet seasons and then concentrate into the riverine savanna during dry seasons, may contribute to the unusually high impala density in this system (Table 16.2). Another potential contributor to high impala density is the nutrient-rich soils occurring along the Chobe riverfront (Skarpe et al. 2014a, b).

#### 16.4.4 Kruger National Park, South Africa

KNP encompasses a broad diversity of savanna communities resulting from underlying variation in soils, topography, and MAP, which varies from 350 to 750 mm. KNP hosts many long-term studies on plant–herbivore interactions that provide a foundation for our understanding of savanna ecology. Exclosures that prevent access by all large herbivores have been in place for >40 years in three locations corresponding to ~400, 600, and 750 mm MAP, with the first two sites on relatively fertile basaltic soils and the third on less fertile granitic soils. Remote sensing of woody canopy structure via LiDAR showed that browsers reduced canopy height and density of woody plants at all sites (Asner et al. 2009). Browser exclusion also substantially altered species composition and size class distributions, with the strongest effects at the most arid site (Wigley et al. 2014). However, the relative contributions of elephants versus mesobrowsers to these outcomes are not clear.

Mesobrowser densities in KNP vary in relation to distance from permanent water (Redfern et al. 2003). In areas near water that support high densities of mesobrowsers and giraffe, pruning of the dominant *A. nigrescens* stimulated regrowth of shoots with enhanced digestibility, thereby creating a feedback to browsers that maintained a “browsing lawn” (Fornara and du Toit 2008). This phenomenon has parallels in the Laikipia, Chobe, and HiP case studies, as intense browsing pressure has largely prevented transition of *A. nigrescens* into large, reproductive size classes. In comparison with *A. nigrescens* stands distant from water, the intensely browsed stands near water exhibited increased shoot growth rates, more stems per crown, and greater root diameters at shallow soil depth (Fornara and du Toit 2008). These responses created a feedback loop that enhanced forage quantity and quality for browsers and maintained resilience of the acacias to browsing impact. Such browsing lawns are important because they are a key resource for browser populations and they sustain the woody layer in a state that can quickly undergo transitions to larger size classes if browsing pressure is temporarily reduced due to other factors (e.g. drought, disease). This highlights the importance of storage effects (*sensu* Higgins et al. 2000) in understanding the long-term dynamics of mesobrowser–woody plant interactions.

The role of mesobrowsers at lower densities (see Kruger [B] in Table 16.2) has been investigated using a pair of exclosures in KNP – one that excludes all herbivores, and one that only excludes elephant and giraffe – located in a mixed fine-leaved and broad-leaved savanna receiving ~550 mm MAP (Scogings et al. 2012, 2013). In the first 5 years of the study, exclusion of all herbivores (but not exclusion of elephant and giraffe alone) resulted in increased woody plant density, compared with outside the exclosures,

primarily due to the response of *D. cinerea*, suggesting that mesobrowsers had more influence than elephants on woody plant density (Scogings et al. 2012). However, compositional changes were not yet evident under either enclosure treatment. Mesobrowsers did not influence sapling height of the dominant *A. grandicornuta* or the rapidly growing *D. cinerea*. Height of two broad-leaved species increased with exclusion of elephant and giraffe, suggesting greater influence of megabrowsers on plant height relative to mesobrowsers (Scogings et al. 2013). Only for *Grewia flavescens* was mean sapling height reduced by mesobrowsers (Scogings et al. 2013). These findings provide an important contrast to the three previous case studies, and emphasize that mesobrowser density estimates associated with enclosure studies are needed to develop a comprehensive understanding of browsing in savannas. In the absence of high mesobrowser density (e.g. no dik-dik or eland, low kudu density, or impala at  $\sim 24 \text{ km}^{-2}$ ), effects on the woody layer are relatively limited and may require decades to detect through enclosure studies. This level of impact, which may be common in African savannas, is likely to favor persistence of woody plants that are relatively fast growing, can compensate for biomass loss at the scale of individual twigs, but still invest moderately in structural defenses to deter browsers.

## 16.5 Evidence from Long-Term Perspectives

Effects of browsers on savanna structure, and the feedbacks from browse availability and habitat structure to mesobrowser populations, are manifest over time scales ranging from years to centuries (Chapters 9 and 15). Thus, measurements of long-term patterns in woody vegetation with respect to mesobrowsers are critical for our understanding of these interactions, despite the inevitable uncertainties that arise from a lack of experimental controls. In one of the first studies to implicate mesobrowsers as drivers of savanna structure, Prins and Van der Jeugd (1993) found that a temporary reduction in impala populations due to an anthrax outbreak corresponded temporally with a cohort of acacias transitioning to larger size classes, and dominating the size class distribution of the savanna for decades after. A pulse in recruitment to large size classes was recently reproduced experimentally (with fences instead of anthrax) by Staver and Bond (2014) in South Africa.

Similar pulses in recruitment of *Acacia* species and establishment of *E. divinorum* thickets during the 1890s–1920s are suggested to have occurred in the Serengeti ecosystem in association with herbivore suppression by the rinderpest epizootic (Sharam et al. 2006). Two enclosure studies in Serengeti provide experimental evidence for this conjecture by showing that mesobrowsers suppress growth of saplings to adults for multiple *Acacia* species (Belsky 1984), as well as *E. divinorum* (Sharam et al. 2006), but the densities and identities of the herbivore species causing these effects were not measured. Although *E. divinorum* is known to have high concentrations of phenolic compounds, and to be largely avoided by mesobrowsers, impala remove apical buds and young shoots of seedlings (Sharam et al. 2006).

Oak savannas of North America provide one of the few areas outside of the tropical savannas where mesobrowsers are suggested to play a role in regulating woody plant balance with grasses. In oak savannas occurring along coastal valleys of western North America, an analysis of historical and recent oak recruitment patterns by MacDougall

(2008) indicates that historic periods of mesobrowser suppression by intensive human hunting (in this case, primarily populations of mule deer, *Odocoileus hemionus*, but also elk, *Cervus elaphus*) coincide with pulsed transitions of oaks into larger size classes, while in the past half-century recruitment has been largely suppressed by mesobrowsers due to reduced hunting pressure. A similar role for white-tailed deer in oak savannas of Texas has been postulated by Russell and Fowler (2002). These patterns mirror the work of Prins and Van der Jeugd (1993) for impala in Africa, but in the case of North American savannas, human hunting, rather than disease, is providing a window of opportunity for woody plant cohorts to reach mature sizes.

Ithala Game Reserve in South Africa provides another long-term perspective on browsers in savannas. In this reserve, changes in woody cover have been examined for >50 years, and changes in woody species composition and size class distribution have been monitored for two decades (Wiseman et al. 2004; Gordijn et al. 2012). Woody plant density declined by 11% in the 1990s (Wiseman et al. 2004), but then increased 3.4-fold in the 2000s (Gordijn et al. 2012). Compositional shifts included 1.5–5.6-fold increases in three *Euclea* species that experienced low browsing pressure, 4.5–6.5-fold increases in *D. cinerea*, *Combretum apiculatum*, and *Berchemia zeyheri*, and a wide range of responses (e.g. –37% to +276%) for different *Acacia* species during 2000–2009 (Gordijn et al. 2012). The less browsed (less palatable) acacias increased. These results indicate an overall shift toward less palatable species (particularly *Euclea*) in the presence of moderate mesobrowser abundance (Table 16.2), but also show that increased rainfall and reduced fire can make the browser filter sufficiently porous to permit recruitment of several palatable species. However, the relative effects of meso- and megabrowsers at Ithala are unclear.

Long-term studies of bush encroachment in Africa also shed light on the role of mesobrowsers in grass–woody balance. In their analysis of an *Acacia*-dominated savanna, with increasing abundance of *D. cinerea*, Roques et al. (2001) found that increasing cattle grazing intensity and a reduction in fire frequency and severity were driving increases in woody cover. However, presence of mesobrowsers (impala, kudu, and goats) also had a significant, secondary influence on woody cover. A similar convergence of intensive cattle grazing, altered fire regimes, and low browser density leading to extensive bush encroachment occurred in a mesic Tanzanian savanna (Tobler et al. 2003). While multiple, interacting factors are driving these outcomes at local scales, these examples provide broader-scale support for conclusions from our case studies, which indicate that sustaining mesobrowsers in savannas can help suppress woody plant encroachment.

## 16.6 The Influence of High Densities of Individual Mesobrowser Species

Our four African case studies revealed significant mesobrowser effects on woody plant regeneration in association with high localized densities of impala (Chobe, HiP) or dikdik (Laikipia). Whether larger mesobrowsers, such as eland and greater kudu, can exert strong feedback effects on the woody plant community is less clear. Long-term studies in KNP suggest that greater kudu populations are regulated by a complex set of factors including dry season rainfall, predation, cold weather, and disease (Owen-Smith and Ogutu 2003; Owen-Smith and Mills 2006), which limit the impact of kudu on wet

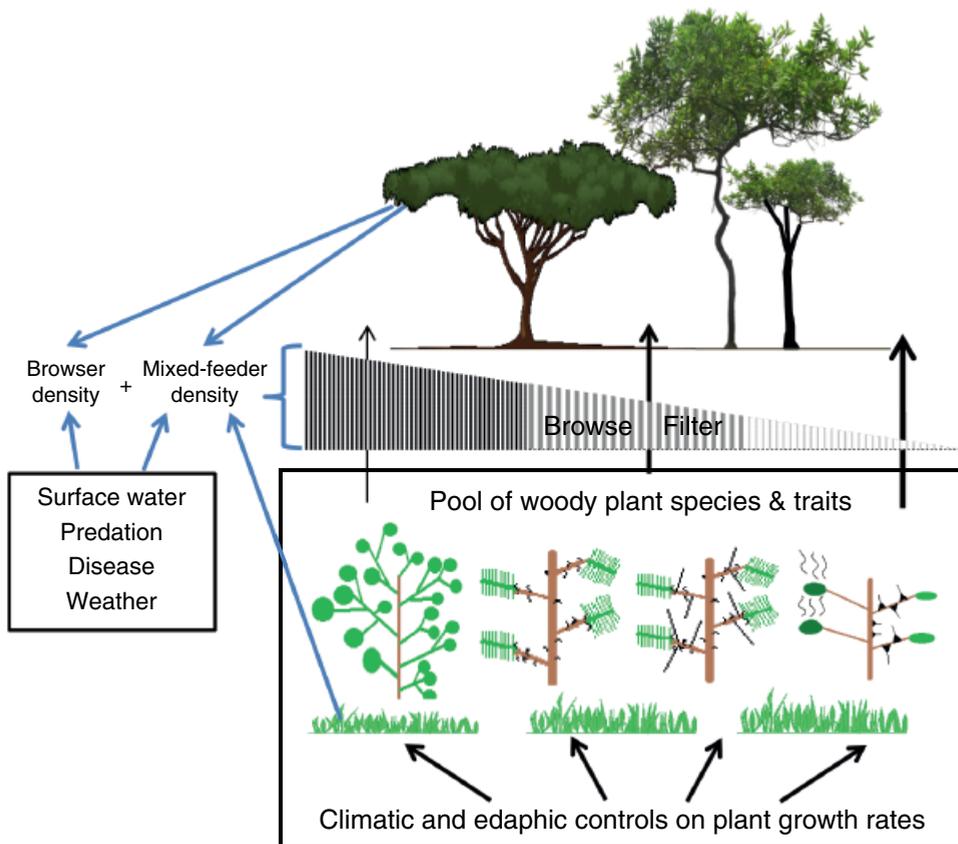
season woody plant growth. In contrast, where high densities of browsers are sustained across wet and dry seasons (e.g. dik-dik, Augustine 2010), substantial impacts on woody plants are likely. Based on our review of African savannas, greater kudu and eland typically occur at low densities and comprise a substantially lower proportion of browser metabolic biomass than co-occurring impala. The highest reported density of 3.2 greater kudu  $\text{km}^{-2}$  at the Tuli Game Reserve was associated with the presence of a dense network of anthropogenic water points, which enhanced impala densities and potentially altered predation patterns on other species. At Tuli, kudu reached a pre-drought density of  $3.6 \text{ km}^{-2}$  and remained at  $2.9 \text{ km}^{-2}$  after a 2-year drought (Walker et al. 1987). The effect of kudu on woody plants under such conditions are not known, but could potentially be significant for plant species that are selectively browsed immediately after drought years, particularly in light of low drought-induced kudu mortality.

One example of eland achieving unusually high densities in association with anthropogenic water points, and in turn impacting woody plant dynamics, comes from a study of a semi-arid (585 mm MAP) *Combretum*-dominated savanna in southern Zimbabwe (Nyengera and Sebata 2009). Here, eland occurred at densities of  $1.9 \text{ km}^{-2}$  in the vicinity of permanent water sources ( $\leq 8 \text{ km}$  radius) and  $0.9 \text{ km}^{-2}$  in areas further from water. In the high density zone,  $\sim 90\%$  of *C. apiculatum* plants had branches broken and apical meristems lost due to eland browsing. Eland reduced mean height of *C. apiculatum* from 5.05 to 2.88 m, prevented recruitment above 5.6 m, and caused extensive stem breakage in lower height classes (Nyengera and Sebata 2009). Although kudu and impala were also present in the study area at unknown densities, this study suggests that the larger mesobrowsers can have important feedback effects on woody plants under localized conditions that permit these species to occur at high densities.

Another example of the effects of exceptional densities of a single mesobrowser species comes from studies of Sand Forest communities in South Africa (Lagendijk et al. 2011, 2012). These closed canopy, edaphically derived forests are surrounded by savannas supporting diverse native ungulates; however, only elephant and nyala occur within the Sand Forest, and the closed canopy likely induces greater importance of light limitation for woody plant growth compared with savannas. Nyala density averaged  $9.7 \text{ km}^{-2}$  across the entire Phinda Game Reserve during the years 2005–2007 (Lagendijk et al. 2011) which is at least four times greater than nyala densities reported for other sites where they occur (Table 16.2); localized nyala densities can be even greater in small patches of Sand Forest within the reserve. Replicated fencing treatments that excluded either elephant alone, or both elephant and nyala, demonstrated that nyala browsing suppressed recruitment of multiple woody species, and nyala effects were even stronger than those of elephants (Lagendijk et al. 2011, 2012). These findings reinforce the idea that where mixed-feeding mesobrowsers occur at high densities, they alter the structure and composition of woody plant communities.

## 16.7 Water, Nutrients, and Mesobrowsers

Mesobrowser abundance varies substantially across African and Asian savannas, and is influenced by a wide range of factors other than the availability of browse within the foraging height of a given species (Figure 16.1). It has long been recognized that the biomass of mammalian herbivores increases with MAP and soil fertility (Bell 1982; East



**Figure 16.1** Conceptual diagram of how mesobrowsers (both mixed-feeders and pure browsers) function as a filter that influences the density and functional species composition of the woody canopy layer in savannas. The four types of saplings depicted in the pool of woody plant species and traits represent the four functional groups in Table 16.1 (ordered left to right in the same way, and representing a gradient of increasing investment in herbivore defense). Recruitment into the canopy layer is dependent upon both the thickness and porosity of the browser filter (determined by mesobrowser abundance and foraging behavior) and by variation among species in growth rate (determined by climatic and edaphic factors). Abundance of mesobrowsers may be uncoupled from the availability of woody foliage within their foraging height due to multiple other factors (blue arrows) including forage inputs from the canopy, herbaceous forage availability, surface water distribution, predation, disease, and weather conditions. (See color plate section for the color representation of this figure.)

1984; Fritz and Duncan 1994). Regions of Africa with nutrient-rich soils tend to support greater abundances of browsing and mixed-feeding ruminants, while nutrient-poor savannas are dominated by bulk-feeding herbivores consisting predominantly of large grazers and megabrowsers (Hempson et al. 2015). This reflects the fact that, compared with grazers, mesobrowsers tend to depend upon higher-quality forage, and include more smaller-bodied species. In some cases, these patterns have also been well quantified at finer spatial resolutions, such as in the Chobe ecosystem where savannas on alluvial soils (pH = 6.2, cation exchange capacity (CEC) = 5.8 meq 100 g<sup>-1</sup> soil) support abundant mesobrowsers with strong feedbacks to woody plant communities while

adjacent savannas on the nutrient-poor Kalahari sand sheet (pH = 5.2, CEC = 2.6 meq 100 g<sup>-1</sup> soil) support few mesobrowsers (Skarpe et al. 2014a).

However, some savannas classified as nutrient-poor in East's (1984) framework, such as KNP and HiP, support moderate to high densities of mesobrowsers that have important effects on woody plant dynamics, as discussed previously. Similarly, the Laikipia case study (where mesobrowsers have particularly strong effects on woody plant communities) occurs on deep, sandy soils developed from basement, metamorphic parent materials that would be classified by East (1984) as low soil nutrient status. These soils have a mean pH of 5.77 and CEC of 13.0 meq 100 g<sup>-1</sup> soil (Augustine et al. 2011). In contrast, adjacent *Acacia drepanolobium*-dominated savannas with similar rainfall occur on high-clay vertisol soils that have similar pH (5.80) and greater CEC (30.3 meq 100 g<sup>-1</sup> soil, excluding H<sup>+</sup>), yet support lower densities of impala and eland, and no dik-dik or kudu (Augustine et al. 2011). Thus, we can generalize that both the mesic, dystrophic savanna regions of Africa identified by Hempson et al. (2015) and the less mesic, but still extremely nutrient-poor savannas, such as those on the Kalahari sands of southern Africa (Chamaille-Jammes 2009; Skarpe et al. 2014a,b), are generally unable to support sufficient mesobrowser densities to have strong feedbacks to woody plant communities. However, for the remaining extensive and often edaphically heterogeneous savannas of Africa, the abundance and influence of mesobrowsers can vary widely in ways unrelated to rainfall and soil nutrient status (Chapter 15).

Our review highlighted several factors, other than ecosystem productivity, that impinge on mesobrowsers. Proximity to, and permanence of, surface drinking water appears to be a key factor influencing the distribution and abundance of impala. Landscapes supporting moderate to high densities of impala typically contain permanent rivers (e.g. Redfern et al. 2003; Moe et al. 2009; Augustine 2010; Ogutu et al. 2014), and augmentation of surface water distribution and permanence can potentially amplify impala and eland effects on woody plants during and following droughts (Walker et al. 1987; Nyengera and Sebata 2009). Conversely, the abundance of some smaller browsers such as dik-dik can be largely independent of surface drinking water and insensitive to seasonal or annual variation in rainfall (Augustine 2010), but strongly dependent upon vegetation structural characteristics that facilitate predator avoidance (Ford and Goheen 2015). Finally, both mixed-feeders and pure browsers can receive forage subsidies in the form of fallen leaves, flowers, and fruits from the canopy layer. Such forage inputs can reduce consumption of seedling and sapling foliage in the short term, but can also increase and stabilize mesobrowser abundance over the long term.

## 16.8 Synthesis

We classified the dominant woody plants studied within the exclosures at the African case study sites into four functional groups that reflect a gradient of increasing investment in anti-browser defenses: (i) unarmed deciduous species, usually with low secondary metabolites, especially phenolics; (ii) spinescent deciduous species with variable, but seldom high phenolics; (iii) unarmed deciduous species with moderate or high phenolics; and (iv) unarmed, usually evergreen species with high phenolics (Table 16.6). These functional groups also represent a gradient of decreasing likelihood of selection by mesobrowsers (Owen-Smith and Cooper 1987). As expected, based on direct effects

**Table 16.6** Effects of mesobrowsers on regeneration of species classified into four woody plant functional groups (derived from Scogings et al. 2011) in four African savanna sites.

Study site	Weighted mesobrowser biomass index (kg km <sup>-2</sup> )	Unarmed, deciduous, usually with low phenolics	Spinescent, deciduous, with variable phenolic concentrations		Unarmed, deciduous, with moderate or high phenolics	Unarmed, usually evergreen, with high phenolics
			Straight or recurved	Both		
(1) Laikipia, Kenya	517	<i>Grewia tenax</i> <sup>a</sup>	<i>Acacia mellifera</i> <sup>b</sup> , <i>Acacia brevispica</i> <sup>b</sup>	<i>Acacia etbaica</i>		<i>Croton dichogamous</i>
(2) Chobe, Botswana	398	<i>Garcinia livingstonei</i> <sup>a</sup>	<i>Faidherbia albida</i> <sup>a</sup> , <i>Combretum mossambicense</i>			<i>Croton megalobotrys</i>
(3) Hluhluwe-iMfolozi, South Africa	354		<i>Ziziphus mucronata</i> <sup>a</sup> , <i>Acacia karroo</i> <sup>b</sup> , <i>Dichrostachys cinerea</i>		<i>Spirostachys africana</i> <sup>a</sup>	<i>Euclea racemosa</i>
(4) Kruger, South Africa	188	<i>Grewia flavescens</i> <sup>a</sup>	<i>D. cinerea</i> <sup>b</sup> , <i>Acacia exuvialis</i> , <i>A. grandicornuta</i>		<i>Combretum apiculatum</i>	<i>Euclea divinorum</i>

(1) Sankaran et al. (2013), (2) Moe et al. (2009), Skarpe et al. (2014b), (3) O’Kane et al. (2014), (4) Fornara and DuToit (2007), and Scogings et al. (2012, 2013).

<sup>a</sup> species eliminated or nearly so by the browser filter;

<sup>b</sup> species suppressed by the browser filter, but still persisting in the sapling layer and potentially into the adult layer; remaining species are not suppressed or increase with mesobrowsers. Sites are listed from (1) to (4) in order of decreasing mesobrowser abundance as calculated in Table 16.5.

of foliage loss to browsers, woody species for which enclosure experiments have demonstrated suppression by mesobrowsers (decreasers; identified by the superscript (a) in Table 16.6) mostly occur in the two functional groups most preferred by mesobrowsers, and at sites with high ( $>300 \text{ kg km}^{-2}$ ) or very high ( $>500 \text{ kg km}^{-2}$ ) mesobrowser metabolic biomass. For these sites, herbivore exclusion allowed these species to increase rapidly in abundance (within less than a decade). In contrast, limited changes in woody plant abundance and species composition have occurred where mesobrowser metabolic biomass is low ( $<200 \text{ kg km}^{-2}$ ).

Increaser species (including ones identified by the superscript (b) in Table 16.6) were more variable in terms of the functional groups in which they occur. These species have increased in abundance in browsed relative to unbrowsed conditions for all mesobrowser densities. Under the intense browsing regime at Chobe, both uneaten and heavily browsed species currently co-dominate the community. At the Laikipia site, which supports the highest measured mesobrowser density, only the most spinescent woody species coexist at stable abundance with browsers, while no species in any other functional groups have increased in the presence of browsers, compared with their absence (Table 16.6). Thus, patterns are clear at the very high ( $>500$ ) and low ( $<200$ ) ends of the weighted biomass index range, but less clear in between. Understanding the role of browsing in savannas will require more nuanced knowledge of edaphic and climatic controls on plant growth, combined with improved understanding of how traits other than defense-related ones affect responses to browsers. Traits that may be important to consider in relation to herbivory include leaf morphology, longevity, and physiology (e.g. Wigley et al. 2014), branching architecture (Chapter 14), variation in the type and costs of secondary metabolites (Chapter 15), and variation in below-ground allocation and resource acquisition patterns (Chapters 11 and 12).

While enclosure studies conducted in a broader range of savanna ecosystems, particularly in southern Asia, are needed to improve our understanding of mesobrowser effects, enclosure experiments alone are insufficient. A key need is the integration of enclosure experiments with studies that quantify (i) mesobrowser abundance at appropriate spatial and temporal scales; (ii) determinants of mesobrowser abundance; (iii) seasonal and spatial variation in herbivore diets in relation to forage availability; and (iv) variation among woody species in resource allocation patterns (e.g. among leaves, spines, branches, roots, and secondary metabolites) and other traits that determine variation in growth rates within a given set of climatic and edaphic conditions (Figure 16.1). We suggest that mesobrowsers function as a filter influencing which suites of traits can persist to the canopy layer, where the thickness and porosity of the filter is determined by mesobrowser abundance and diet composition. Fortunately, the increasingly widespread adoption of ground-based distance-sampling procedures has provided improved measures of herbivore abundance in dense vegetation (see sources in Tables 16.2 and 16.3). Furthermore, new technologies for quantifying herbivore diet composition (e.g. Kartzinzel et al. 2015) can provide key insights to foraging selectivity, provided they are combined with measures of plant species availability within the foraging environment. Finally, understanding of the drivers of variation in quantitative functional traits is advancing (e.g. Tomlinson et al. 2016).

Overall, our synthesis shows that mesobrowsers operate as a filter that strongly influences the rate and composition of woody plant recruitment into the canopy layer in

African savannas (Figure 16.1). These effects can occur over temporal scales of less than a decade where weighted mesobrowser metabolic biomass exceeds  $300 \text{ kg km}^{-2}$  (Table 16.6). A wide range of woody plant functional groups can persist, or increase, under intense browsing, including palatable broad-leaved species, palatable spinescent species with varying levels of armament investment, and unpalatable broad-leaved species. Additional layers of complexity we have not addressed are generated by the effects of grazers on fire regimes and grass–tree competition. Traits related to woody plant fire resistance (Staver et al. 2012) and below-ground resource acquisition are among those that potentially interact with investment in herbivore defense to influence woody plant growth rate and passage through the browser filter.

In African savannas, recognition of these mesobrowser effects has important implications for where and how elephant and water source management influence vegetation dynamics. Feedbacks between woody plant communities and long-term mesobrowser abundance will also have consequences for carnivore conservation, particularly for leopards (*Panthera pardus*) and African wild dogs (Woodroffe et al. 2007; Moe et al. 2014). In tropical savannas beyond Africa, mesobrowser density estimates suggest that their role is relatively minimal in Neotropical and Australasian savannas, but may be substantial in Asian savannas. Feedbacks between mesobrowsers and woody plants in Asian savannas also have implications for management of the prey base for lion (*Panthera leo*) and tiger (*Panthera tigris*) conservation (Karanth et al. 2004; Singh and Gibson 2011). Research on interactions between mesobrowsers and woody plants in Asian savannas is clearly needed, and could provide broad insights into savanna ecosystem dynamics when conducted in light of our current understanding of mesobrowsers in African savannas.

## Acknowledgments

We thank Kyler Sherry for assistance with literature reviews. The United States Department of Agriculture Agricultural Research Service (USDA-ARS), University of Zululand, and the National Centre for Biological Sciences, India, provided support for the authors during preparation of this chapter.

## References

- Ahrestani, F.S., Heitkönig, I.M.A., and Prins, H.H.T. (2012). Diet and habitat-niche relationships within an assemblage of large herbivores in a seasonal tropical forest. *Journal of Tropical Ecology* 28: 385–394.
- Amubode, F.O. and Boshe, J.I. (1990). Assessment of permanence and stability in the territories of Kirk's dikdik (*Rhynchotragus kirki*) in Tanzania. *Journal of Tropical Ecology* 6: 153–162.
- Asner, G.P., Levick, S.R., Kennedy-Bowdoin, T. et al. (2009). Large-scale impacts of herbivores on the structural diversity of African savannas. *Proceedings of the National Academy of Sciences* 167: 4947–4952.
- Augustine, D.J. (2010). Response of native ungulates to drought in semi-arid Kenyan rangeland. *African Journal of Ecology* 48: 1009–1020.

- Augustine, D.J. and McNaughton, S.J. (1998). Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *Journal of Wildlife Management* 62: 1165–1183.
- Augustine, D.J. and McNaughton, S.J. (2004). Regulation of shrub dynamics by native browsing ungulates on East African rangeland. *Journal of Applied Ecology* 41: 45–58.
- Augustine, D.J., Veblen, K., Goheen, J. et al. (2011). Pathways for positive cattle-wildlife interactions in semiarid rangelands. In: *Conserving Wildlife in African Landscapes: Kenya's Ewaso Ecosystem* (ed. N. Geogiadis), 55–71. Washington, DC: Smithsonian Institution Scholarly Press.
- Bagchi, S. (2003). Niche relationships of an ungulate assemblage in a dry tropical forest. *Journal of Mammalogy* 84: 981–988.
- Bagchi, S., Goyal, S.P., and Sankar, K. (2004). Herbivore density and biomass in a semi-arid tropical dry deciduous forest of Western India. *Journal of Tropical Ecology* 20: 475–478.
- Baskaran, N., Kannan, V., Thiyagesan, K., and Desai, A.A. (2011). Behavioural ecology of four-horned antelope (*Tetracerus quadricornis* de Blainville, 1816) in the tropical forests of southern India. *Mammalian Biology* 76: 741–747.
- Bell, R.H.V. (1982). The effect of soil nutrient availability on community structure in African ecosystems. In: *Ecology of Tropical Savannas* (ed. B.J. Huntley and B.H. Walker), 193–216. New York: Springer-Verlag.
- Belsky, A.J. (1984). Role of small browsing mammals in preventing woodland regeneration in the Serengeti National Park, Tanzania. *African Journal of Ecology* 22: 271–279.
- Bhat, S.A., Telang, S., Wani, M.A., and Sheikh, K.A. (2012). Food habits of nilgai (*Boselaphus tragocamelus*) in Van Vihar National Park, Bhopal, Madhya Pradesh, India. *Biomedical and Pharmacology Journal* 5: 141–157.
- Bhola, N., Ogutu, J.O., Piepho, H.P. et al. (2012). Comparative changes in density and demography of large herbivores in the Masai Mara Reserve and its surrounding human-dominated pastoral ranches in Kenya. *Biodiversity and Conservation* 21: 1509–1530.
- Bista, A. (2011). Proximate determinants of ungulate distribution and abundance in Pilibhit Forest Division, Uttar Pradesh, India. Master's Thesis, Wildlife Institute of India.
- Biswas, S. and Sankar, K. (2002). Prey abundance and food habit of tigers (*Panthera tigris tigris*) in Pench National Park, Madhya Pradesh, India. *Journal of Zoology* 256: 411–420.
- Bowman, D.M.J.S., Brown, G.K., Braby, M.F. et al. (2010). Biogeography of the Australian monsoon tropics. *Journal of Biogeography* 37: 201–216.
- Cerling, T.E., Harris, J.M., and Passey, B.H. (2003). Diets of East African Bovidae based on stable isotope analysis. *Journal of Mammalogy* 84: 456–470.
- Chamaille-Jammes, S. (2009). Seasonal density estimates of common large herbivores in Hwange National Park, Zimbabwe. *African Journal of Ecology* 47: 804–808.
- Coates-Palgrave, M. (2002). *Trees of Southern Africa*, 3rd ed. Cape Town: Struik Publishers.
- Codron, D., Codron, J., Lee-Thorp, J.A. et al. (2007). Diets of savanna ungulates from stable carbon isotope composition of faeces. *Journal of Zoology* 273: 21–29.
- Dantas, V.L. and Pausas, J.G. (2013). The lanky and the corky: fire-escape strategies in savanna woody species. *Journal of Ecology* 101: 1265–1272.
- Dawson, T.J. (1995). *Kangaroos*. Sydney, Australia: University of New South Wales Press.
- DeGabriel, J.L., Moore, B.D., Foley, W.J., and Johnson, C.N. (2009). The effects of plant defensive chemistry on nutrient availability predict reproductive success in a mammal. *Ecology* 90: 711–719.

- Desbiez, A.L.J., Bodmer, R.E., and Tomas, W.M. (2010). Mammalian densities in a Neotropical wetland subject to extreme climatic events. *Biotropica* 42: 372–378.
- Dinerstein, E. (1979). An ecological survey of the Royal Karnali-Bardia Wildlife Reserve, Nepal. Part I: vegetation, modifying factors and successional relationships. *Biological Conservation* 15: 127–150.
- Dinerstein, E. (1980 [1979]). An ecological survey of the Royal Karnali-Bardia Wildlife Reserve, Nepal. Part III: ungulate populations. *Biological Conservation* 18: 5–37.
- East, R. (1984). Rainfall, soil nutrient status and biomass of large African savanna mammals. *African Journal of Ecology* 22: 245–270.
- Fisher, M.J. and Kerridge, P.C. (1996). The agronomy and physiology of *Brachiaria* species. In: *Brachiaria Biology, Agronomy, and Improvement* (ed. J.W. Miles, B.L. Maass and C.B. do Valle), 43–62. Campo Grande, Brazil: Centro Internacional de Agricultura Tropical (CIAT).
- Ford, A.T. and Goheen, J.R. (2015). An experimental study on risk effects in a dwarf antelope, *Madoqua guentheri*. *Journal of Mammalogy* 96: 918–926.
- Ford, A.T., Goheen, J.R., Augustine, D.J. et al. (2015). Recovery of African wild dogs suppresses prey but does not trigger a trophic cascade. *Ecology* 96: 2705–2714.
- Ford, A.T., Goheen, J.R., Otieno, T.O. et al. (2014). Large carnivores make savanna tree communities less thorny. *Science* 346: 346–349.
- Fornara, D.A. and du Toit, J.T. (2007). Browsing lawns? Responses of *Acacia nigrescens* to ungulate browsing in an African savanna. *Ecology* 88: 200–209.
- Fornara, D.A. and Du Toit, J.T. (2008). Responses of woody saplings exposed to chronic mammalian herbivory in an African savanna. *Ecoscience* 15: 129–135.
- Fritz, H. and Duncan, P. (1994). On the carrying capacity for large ungulates of African savanna ecosystems. *Proceedings of the Royal Society of London, Series B* 256: 77–82.
- Fritz, H., Duncan, P., Gordon, I., and Illius, A. (2002). Megaherbivores influence trophic guilds structure in African ungulate communities. *Oecologia* 131: 620–625.
- Gopal, R., Qureshi, Q., Bhardwaj, M. et al. (2010). Evaluating the status of the endangered tiger *Panthera tigris* and its prey in Panna Tiger Reserve, Madhya Pradesh, India. *Oryx* 44: 383–389.
- Gordijn, P.J., Rice, E., and Ward, D. (2012). The effects of fire on woody plant encroachment are exacerbated by succession of trees of decreased palatability. *Perspectives in Plant Ecology, Evolution and Systematics* 14: 411–422.
- Hempson, G.P., Archibald, S., and Bond, W.J. (2015). A continent-wide assessment of the form and intensity of large mammal herbivory in Africa. *Science* 350: 1056–1061.
- Hester, A.J., Scogings, P.F., and Trollope, W.S.W. (2006). Long-term impacts of goat browsing on bush-clump dynamics in a semi-arid subtropical savanna. *Plant Ecology* 183: 277–290.
- Higgins, S.I., Bond, W.J., and Trollope, W.S.W. (2000). Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. *Journal of Ecology* 88: 213–229.
- Ismail, D. and Jiwan, D. (2015). Browsing preference and ecological carrying capacity of sambar deer (*Cervus unicolor brookei*) on secondary vegetation in forest plantation. *Animal Science Journal* 86: 225–237.
- Jachmann, H. (2002). Comparison of aerial counts with ground counts for large African herbivores. *Journal of Applied Ecology* 39: 841–852.
- Karanth, K.U. and Nichols J.D. (2000). Ecological status and conservation of tiger in India. Final Technical Report to the Division of International Conservation. US Fish and

- Wildlife Service, Washington, DC and Wildlife Conservation Society, New York. Centre for Wildlife Studies, Bangalore, India.
- Karanth, K.U. and Sunquist, M.E. (1992). Population structure, density and biomass of large herbivores in the tropical forests of Nagarahole, India. *Journal of Tropical Ecology* 8: 21–35.
- Karanth, K.U., Nichols, J.D., Kumar, N.S. et al. (2004). Tigers and their prey: predicting carnivore densities from prey abundance. *Proceedings of the National Academy of Sciences of the United States of America* 101: 4854–4858.
- Kartzinel, T.R., Chen, P.A., Coverdale, T.C. et al. (2015). DNA metabarcoding illuminates dietary niche partitioning by African large herbivores. *Proceedings of the National Academy of Sciences of the United States of America* 112: 8019–8024.
- Khan, J.A., Chellam, R., Rodgers, W.A., and Johnsingh, A.J.T. (1996). Ungulate densities and biomass in the tropical dry deciduous forests of Gir, Gujarat, India. *Journal of Tropical Ecology* 12: 149–162.
- Komers, P. and Brotherton, P. (1997). Dung pellets used to identify the distribution and density of dik-dik. *African Journal of Ecology* 35: 124–132.
- Kumara, H.N., Rathnakumar, S., Sasi, R., and Singh, M. (2012). Conservation status of wild mammals in Biligiri Rangaswamy Temple Wildlife Sanctuary, the Western Ghats, India. *Current Science* 103: 933–940.
- Labisky, R.F., Hurd, C., Oli, M.K., and Barwick, R.S. (2003). Foods of white-tailed deer in the Florida everglades: the significance of *Crinum*. *Southeastern Naturalist* 2: 261–270.
- Legendijk, D.D.G., Mackey, R.L., Page, B.R., and Slotow, R. (2011). The effects of herbivory by a mega- and mesoherbivore on tree recruitment in Sand Forest, South Africa. *PLoS One* 6: e17983.
- Legendijk, G., Page, B.R., and Slotow, R. (2012). Short-term effects of single species browsing release by different-sized herbivores on sand forest vegetation community, South Africa. *Biotropica* 44: 63–72.
- Lehmann, C.E.R., Anderson, T.M., Sankaran, M. et al. (2014). Savanna vegetation-fire-climate relationships differ among continents. *Science* 343: 548–552.
- Leuthold, W. and Leuthold, B.M. (1976). Density and biomass of ungulates in Tsavo East National Park, Kenya. *East African Wildlife Journal* 14: 49–58.
- MacDougall, A.S. (2008). Herbivory, hunting and long-term vegetation change in degraded savanna. *Biological Conservation* 141: 2174–2183.
- Madhusudan, M.D. (2003). Living amidst large wildlife: livestock and crop depredation by large mammals in the interior villages of Bhadra Tiger Reserve, South India. *Environmental Management* 31: 466–475.
- Makhabu, S.W. (2005). Resource partitioning within a browsing guild in a key habitat, the Chobe Riverfront, Botswana. *Journal of Tropical Ecology* 21: 641–649.
- Marquis, R.J., Morais, H.C., and Diniz, I.R. (2002). Interactions among Cerrado plants and their herbivores: unique or typical? In: *The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna* (ed. P.S. Oliveira and R.J. Marquis), 306–328. New York: Columbia University Press.
- McInnes, P.F., Naiman, R.J., Pastor, J., and Cohen, Y. (1992). Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. *Ecology* 73: 2059–2075.
- Miranda, M., Dalerum, F., and Parrini, F. (2014). Interaction patterns within a multi-herbivore assemblage derived from stable isotopes. *Ecological Complexity* 20: 51–60.

- Moe, S.R., Rutina, L.P., Hytteborn, H., and Du Toit, J.T. (2009). What controls woodland regeneration after elephants have killed the big trees. *Journal of Applied Ecology* 46: 223–230.
- Moe, S.R., Rutina, L.P., Hytteborn, H., and Du Toit, J.T. (2014). Impala as controllers of elephant-driven change within a savanna ecosystem. In: *Elephants and Savanna Woodland Ecosystems: A Study from Chobe National Park, Botswana* (ed. C. Skarpe, J.T. Du Toit and S.R. Moe), 154–171. Hoboken, NJ: Wiley Blackwell.
- Mosugelo, D.K., Moe, S.R., Ringrose, S., and Nellemann, C. (2002). Vegetation changes during a 36-year period in northern Chobe National Park, Botswana. *African Journal of Ecology* 40: 232–240.
- Nyengera, R. and Sebata, A. (2009). Effect of eland density and foraging on *Combretum apiculatum* physiognomy in a semi-arid savannah. *African Journal of Ecology* 48: 45–50.
- Ogutu, J.O., Owen-Smith, N., Piepho, H.P. et al. (2012). Dynamics of ungulates in relation to climatic and land use changes in an insularized African savanna ecosystem. *Biodiversity and Conservation* 21: 1033–1053.
- Ogutu, J.O., Reid, R.S., Piepho, H.P. et al. (2014). Large herbivore responses to surface water and land use in an East African savanna: implications for conservation and human-wildlife conflicts. *Biodiversity and Conservation* 23: 573–596.
- O’Kane, C.A.J., Duffy, K.J., Page, B.R., and MacDonald, D.W. (2011). Overlap and seasonal shifts in use of woody plant species amongst a guild of savanna browsers. *Journal of Tropical Ecology* 27: 249–258.
- O’Kane, C.A.J., Duffy, K.J., Page, B.R., and MacDonald, D.W. (2012). Heavy impact on seedlings by the impala suggests a central role in woodland dynamics. *Journal of Tropical Ecology* 28: 291–297.
- O’Kane, C.A.J., Duffy, K.J., Page, B.R., and MacDonald, D.W. (2013). Effects of resource limitation on habitat usage by the browser guild in Hluhluwe-iMfolozi Park, South Africa. *Journal of Tropical Ecology* 29: 39–47.
- O’Kane, C.A.J., Duffy, K.J., Page, B.R., and MacDonald, D.W. (2014). Model highlights likely long-term influences of mesobrowsers versus those of elephants on woodland dynamics. *African Journal of Ecology* 52: 192–208.
- Owen-Smith, N. (1992). *Megaherbivores: The Influence of Very Large Body Size on Ecology*. Cambridge: Cambridge University Press.
- Owen-Smith, N. (2013). Contrasts in the large herbivore faunas of the southern continents in the late Pleistocene and the ecological implications for human origins. *Journal of Biogeography* 40: 1215–1224.
- Owen-Smith, N. and Cooper, S.M. (1987). Palatability of woody plants to browsing ruminants in a South African Savanna. *Ecology* 68: 319–331.
- Owen-Smith, N. and Mills, M.G.L. (2006). Manifold interactive influences on the population dynamics of a multispecies ungulate assemblage. *Ecological Monographs* 76: 73–92.
- Owen-Smith, N. and Ogutu, J.O. (2003). Rainfall influences on ungulate population dynamics. In: *The Kruger Experience: Ecology and Management of Savanna Heterogeneity* (ed. J.T. Du Toit, K. Rogers and H.C. Biggs), 310–331. Washington, DC: Island Press.
- Pokharel, K., Ludwig, T., and Storch, I. (2015). Spatial niche partitioning in sub-tropical solitary ungulates: four-horned antelope and barking deer in Nepal. *PLoS One* 10: 1–16.
- Prins, H.H.T. and Van Der Juegd, H.P. (1993). Herbivore population crashes and woodland structure in East Africa. *Journal of Ecology* 81: 305–314.

- Ramesh, T. (2010). Prey selection and food habits of large carnivores: tiger *Panthera tigris*, leopard *Panthera pardus* and dhole *Cuon alpinus* in Mudumalai Tiger Reserve, Tamil Nadu. PhD Thesis, Saurashtra University, Gujarat, India.
- Ramesh, T., Sankar, K., Qureshi, Q., and Kalle, R. (2012). Group size, sex and age composition of chital (*Axis axis*) and sambar (*Rusa unicorn*) in a deciduous habitat of western Ghats. *Mammalian Biology* 77: 53–59.
- Ratnam, J., Bond, W.J., Fensham, R.J. et al. (2011). When is a “forest” a savanna, and why does it matter? *Global Ecology and Biogeography* 20: 653–660.
- Redfern, J.V., Grant, R., Biggs, H., and Getz, W.M. (2003). Surface-water constraints on herbivore foraging in the Kruger National Park, South Africa. *Ecology* 84: 2092–2107.
- Reilly, B.K. (2002). Precision of helicopter-based total-area counts of large ungulates in bushveld. *Koedoe* 45: 77–83.
- Ritchie, E.G., Martin, J.K., Krockenberger, A.K. et al. (2008). Large-herbivore distribution and abundance: intra and interspecific nich variation in the tropics. *Ecological Monographs* 78: 105–122.
- Roques, K.G., O’Connor, T.G., and Watkinson, A.R. (2001). Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology* 38: 268–280.
- Russell, F.L. and Fowler, N.L. (2002). Failure of adult recruitment in *Quercus buckleyi* populations on the eastern Edwards Plateau, Texas. *American Midland Naturalist* 148: 201–217.
- Rutina, L.P. (2004). *Impalas in an elephant-impacted woodland: browser-driven dynamics of the Chobe riparian zone, northern Botswana*. PhD Thesis, Agricultural University of Norway, Ås, Norway.
- Sankaran, M. (2001). Disturbance, diversity and community dynamics in a southern Indian savanna-grassland ecosystem. PhD Thesis, Syracuse University, Syracuse.
- Sankaran, M., Augustine, D.J., and Ratnam, J. (2013). Native ungulates of diverse body sizes collectively regulate long-term woody plant demography and structure of a semi-arid savanna. *Journal of Ecology* 101: 1389–1399.
- Sankaran, M. and Ratnam, J. (2013). African and Asian savannas. In: *Encyclopedia of Biodiversity*, 2e (ed. S. Levin) (Editor-in-Chief), 58–74. London: Elsevier Press.
- Sankaran, M., Hanan, N.P., Scholes, R.J. et al. (2005). Determinants of woody cover in African savannas. *Nature* 438: 846–849.
- Sankaran, M., Ratnam, J., and Hanan, N.P. (2008). Woody cover in African savannas: the role of resources, fire and herbivory. *Global Ecology and Biogeography* 17: 236–245.
- Schaller, G.B. (1967). *The Deer and the Tiger*. Chicago, IL: University of Chicago Press.
- Scholtz, R., Kiker, G.A., Smit, I.P.J., and Venter, F.J. (2014). Identifying drivers that influence the spatial distribution of woody vegetation in Kruger National Park, South Africa. *Ecosphere* 5: 1–12.
- Scogings, P.F., Hjältén, J., and Skarpe, C. (2011). Secondary metabolites and nutrients of woody plants in relation to browsing intensity in African savannas. *Oecologia* 167: 1063–1073.
- Scogings, P.F., Johansson, T., Hjältén, J., and Kruger, J. (2012). Responses of woody vegetation to exclusion of large herbivores in semi-arid savannas. *Austral Ecology* 37: 56–66.

- Scogings, P.F., Hjältén, J., and Skarpe, C. (2013). Does large herbivore removal affect secondary metabolites, nutrients and shoot length in woody species in semi-arid savannas. *Journal of Arid Environments* 88: 4–8.
- Scogings, P.F., Hjältén, J., Skarpe, C. et al. (2014). Nutrient and secondary metabolite concentrations in a savanna are independently affected by large herbivores and shoot growth rate. *Plant Ecology* 215: 73–82.
- Sharam, G., Sinclair, A.R.E., and Turkington, R. (2006). Establishment of broad-leaved thickets in Serengeti, Tanzania: the influence of fire, browsers, grass competition, and elephants. *Biotropica* 38: 599–605.
- Sharma, K., Rahmani, A.R., and Chundawat, R.S. (2009). Natural history observations of the four-horned antelope *Tetracerus quadricornis*. *Journal of the Bombay Natural History Society* 106: 72–82.
- Singh, H.S. and Gibson, L. (2011). A conservation success story in the otherwise dire megafauna extinction crisis: the Asiatic lion (*Panthera leo persica*) of Gir forest. *Biological Conservation* 144: 1753–1757.
- Skarpe, C., Aarrestad, P.A., Andreassen, H.P. et al. (2004). The return of the giants: ecological effects of an increasing elephant population. *Ambio* 33: 276–282.
- Skarpe, C., Masunga, G., Aarrestad, P.A., and Frost, P.G.H. (2014a). Soil as controller of and responder to elephant activity. In: *Elephants and Savanna Woodland Ecosystems: A Study from Chobe National Park, Botswana* (ed. C. Skarpe, J.T. Du Toit and S.R. Moe), 135–153. Oxford: Wiley Blackwell.
- Skarpe, C., Moe, S.R., Wallgren, M., and Stokke, S. (2014b). Elephants and the grazing and browsing guilds. In: *Elephants and Savanna Woodland Ecosystems: A Study from Chobe National Park, Botswana* (ed. C. Skarpe, J.T. Du Toit and S.R. Moe), 207–228. Oxford: Wiley Blackwell.
- Solanki, G.S. and Naik, R.M. (1998). Grazing interactions between wild and domestic herbivores. *Small Ruminant Research* 27: 231–235.
- Sponheimer, M., Grant, C.C., de Ruiter, D.J. et al. (2003). Diets of impala from Kruger National Park: evidence from stable carbon isotopes. *Koedoe* 46: 101–106.
- Staver, A.C. and Bond, W.J. (2014). Is there a “browse trap”? Dynamics of herbivore impacts on trees and grasses in an African savanna. *Journal of Ecology* 102: 595–602.
- Staver, A.C., Bond, W.J., Stock, W.D. et al. (2009). Browsing and fire interact to suppress tree density in an African savanna. *Ecological Applications* 19: 1909–1919.
- Staver, A.C., Bond, W.J., Cramer, M.D., and Wakeling, J.L. (2012). Top-down determinants of niche structure and adaptation among African *Acacias*. *Ecology Letters* 15: 673–679.
- Tilghman, N.G. (1989). Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. *Journal of Wildlife Management* 53: 524–532.
- Tobler, M.W., Cochard, R., and Edwards, P.J. (2003). The impact of cattle ranching on large-scale vegetation patterns in a coastal savanna in Tanzania. *Journal of Applied Ecology* 40: 430–444.
- Tomlinson, K.W., van Langevelde, F., Ward, D. et al. (2016). Defence against vertebrate herbivores trades off into architectural and low nutrient strategies amongst savanna Fabaceae species. *Oikos* 125 (1): 126–136.
- Walker, B.H., Emslie, R.H., Owen-Smith, R.N., and Scholes, R.J. (1987). To cull or not to cull: lessons from a southern African drought. *Journal of Applied Ecology* 24: 381–401.

- Wigley, B.J., Fritz, H., Coetsee, C., and Bond, W.J. (2014). Herbivores shape woody plant communities in the Kruger National Park: lessons from three long-term exclosures. *Koedoe* 56: 1–12.
- Wiseman, R., Page, B.R., and O'Connor, T.G. (2004). Woody vegetation change in response to browsing in Ithala Game Reserve, South Africa. *South African Journal of Wildlife Research* 34: 25–37.
- Woodroffe, R., Lindsey, P., Romanach, S., and Ole Ranah, S. (2007). African wild dogs (*Lycaon pictus*) can subsist on small prey: implications for conservation. *Journal of Mammalogy* 88: 181–193.