

Chapter 15

The Ecology of Browsing and Grazing in Other Vertebrate Taxa



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Since the publication of the “The Ecology of Browsing and Grazing” (Gordon and Prins 2008), a number of researchers have taken the approach outlined in the book to assess the impacts of differences in food and nutrient supply on the ecology of other vertebrate taxa. The approach may not work in all vertebrate taxa but understanding the similarities and differences between herbivorous vertebrate taxa provides ecologists with a broader canvas upon which to develop and test hypotheses about herbivore/plant interactions. In line with the slightly altered emphasis of the current book (The Ecology of Browsing and Grazing II), we also asked the authors of the

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Sections in this Chapter to provide insights into the impacts that these different vertebrate taxa have on the ecosystems in which they exist. In this Chapter, the authors describe the findings from this research. As you will see, the depth of research on the ecology and impacts of the different herbivorous vertebrate taxa varies considerably and demonstrates the importance of further research endeavours, on herbivore/plant interactions, across the board. The taxa covered are:

- Dinosaurs (Jordan Mallon)
- Fish (Laura D. Puk)
- Reptiles (Everton B. P. Miranda and Carolina Starling-Manne)
- Birds (René van der Wal)
- Marsupials (Ben Moore and William Foley)
- Lagomorphs (Lucy Lush)
- Rodents (Renan Maestri)
- Primates (Ikki Matsuda and Marcus Clauss)

15.1 Dinosaurs

Jordan Mallon

The browser-grazer continuum is not one that readily applies to the non-avian dinosaurs (hereafter, simply ‘dinosaurs’). Although grasses (Poaceae) had evolved by the Cretaceous (Prasad et al. 2005), they were not abundant and did not form

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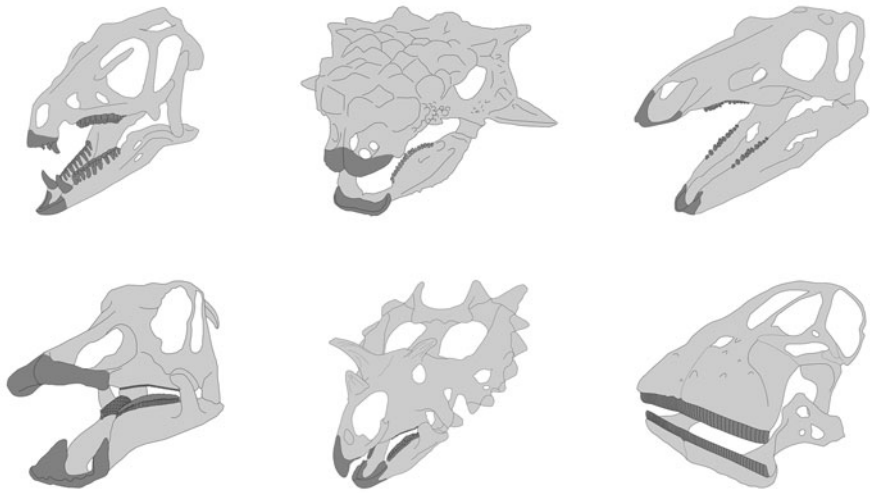
widespread grasslands until the Miocene (Potts and Behrensmeyer 1992). It, therefore, makes little sense to speak of dinosaurian ‘grazers’ *sensu stricto* (but see ‘True Dinosaurian Grazers?’ below). Rather, lycopods, ferns, sphenopsids, cycadophytes, ginkgos, conifers, and (non-poacean) angiosperms made up the bulk of the plant material available for dinosaurian consumption (Gee 2011; Tiffney 2012). Ferns, in particular, likely filled the role of low growing, herbaceous colonizers for most of the Mesozoic (Wing et al. 1993; Collinson 1996). For this reason, it makes more sense to speak of herbivorous dinosaurs in terms of concentrate, intermediate, and bulk feeders (*sensu* Hofmann and Stewart 1972, Mallon and Anderson 2014a).

15.1.1 *Size and Shape*

Whether particular herbivorous dinosaurs were concentrate, intermediate, or bulk feeders would have been primarily influenced by their respective body sizes (Peters 1983). Dinosaur body mass spanned seven orders of magnitude (Benson et al. 2014), so these animals undoubtedly adopted a variety of feeding strategies. Small (10–100 kg) herbivores—including heterodontosaurids, small ornithopods, early thyreophorans, most pachycephalosaurs, and basal ceratopsians, among others—almost certainly concentrated on nutritious shoots, fruits, and seeds to fuel a relatively high metabolism (Weishampel 1984). These dinosaurs were obligatory bipeds, and possessed narrow, pointed beaks with which to selectively crop their food (Coe et al. 1987). Their teeth, and associated jaw mechanics, varied from the simple to the complex, indicative of corresponding variability in dietary fibre intake (Norman and Weishampel 1985; Nabavizadeh 2016) (Fig. 15.1a). Some derived clades developed rudimentary tooth batteries having a single, continuous occlusal surface (e.g., Norman et al. 2011). The jaw joint was depressed below the plane of occlusion, increasing the lever arm of the external mandibular adductor musculature, enabling a more powerful bite. This system was functionally equal, but mechanically opposite, to that of ungulates, where the jaw joint is positioned above the occlusal plane to increase the lever arm of the masseter musculature (Greaves 1995). One lineage, the Ornithopoda, is traditionally thought to have developed a ‘pleurokinetic’ skull having multiple, mobile intracranial joints, allowing the upper jaw to flex laterally during tooth occlusion, to accommodate the lower cheek teeth. Given the isognathous nature of the jaws (where the teeth occlude on both sides when the jaws are closed), this would have resulted in a transverse power stroke, functionally analogous to that of ungulates (Norman and Weishampel 1985). This hypothesis has recently received some push-back—Rybczynski et al. (2008) and Cuthbertson et al. (2012) showed that the secondary intracranial movements imposed by the pleurokinetic model could not be accommodated by the corresponding joints. Rather, minimal rotation of the lower jaw rami, about their long axes, would have produced a similar power stroke, and is mechanically more feasible (Nabavizadeh and Weishampel 2016).

At the opposite end of the size spectrum, megaherbivorous dinosaurs ($\geq 1 \times 10^3$ kg; *sensu* Owen-Smith 1988) included most sauropodomorphs, stegosaurs, ceratopsids, ankylosaurs, and iguanodontians. These forms were highly variable in

A



B

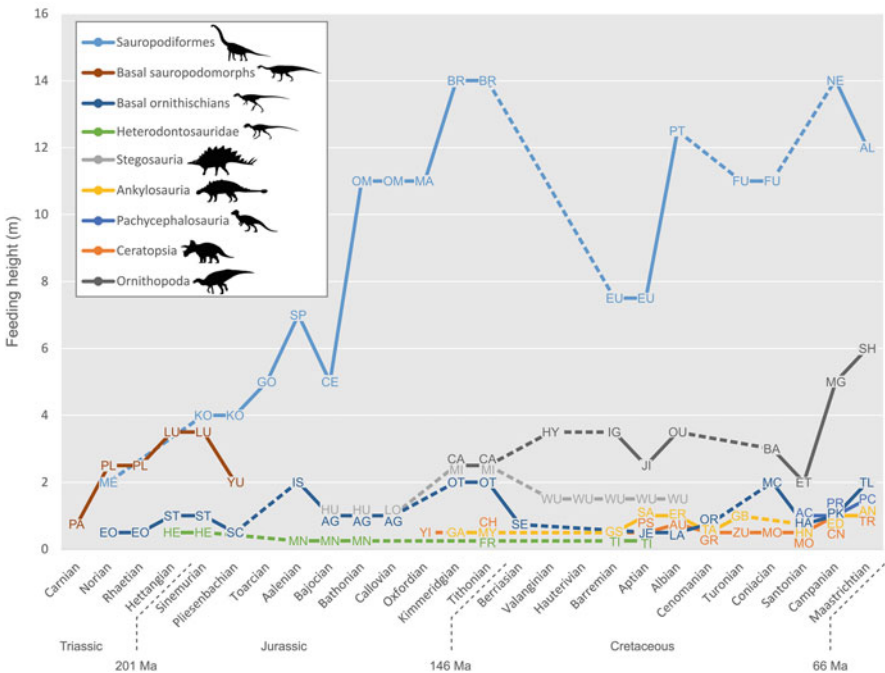


Fig. 15.1 Herbivorous dinosaur ecomorphology. A, Herbivorous dinosaur craniodental adaptations, with beaks and teeth in dark grey (clockwise from upper left): heterodontosaurid, ankylosaur, stegosaur, sauropod, ceratopsian, hadrosaur (skulls not to scale). B, Herbivorous dinosaur feeding heights through time. Sauropodiform feeding heights (assuming vertical necks) were calculated following Upchurch and Barrett (2000). The methodology of Mallon et al. (2013) was used for calculating bipedal feeding heights for basal sauropodomorphs, basal ornithischians,

morphology, and shared few ecomorphological features in common beyond large body size and minimally facultative quadrupedality. Stegosaur and ankylosaur retained primitively small, phylliform teeth, although the beaks of the latter were wider, and presumably predisposed to bulk feeding (Mallon and Anderson 2014a; Ósi et al. 2017). The exceptionally wide bellies of the ankylosaurs attest to lengthy gut-retention times and a preference for fibrous roughage (Bakker 1986).

Iguanodontians and ceratopsids both possessed complex dental batteries, but these functioned in quite different ways. Iguanodontian dental batteries, best exemplified by the hadrosaurids, consisted of hundreds of highly complex, tightly-spaced teeth, multiple rows of which contributed to the occlusal surface (Erickson et al. 2012; LeBlanc et al. 2016). This inclined surface was capable of both crushing and shearing functions. Tooth wear evidence further suggests some capacity for fore-aft grinding (Williams et al. 2009; Mallon and Anderson 2014b). This suite of functions would have allowed the hadrosaurids to rend all manner of plant types, substantiating their inferred role as herbivore generalists. By contrast, the tooth batteries of the ceratopsids were simpler, and the continuous occlusal surface of the teeth was limited to the vertical plane. Thus, ceratopsids were evidently more restricted in their diets, which is consistent with their narrow, selective beaks (Mallon and Anderson 2014a). In this sense, ceratopsids might be likened to the narrow-lipped black rhinoceros, *Diceros bicornis*, which selects for low-growing woody scrub (Owen-Smith 1988).

Largest of all were the sauropodomorphs, with some forms possibly approaching 90 tonnes (Benson et al. 2014). These were characterized by exceedingly long necks ending in proportionally tiny heads. The jaws were simple in construction, and the teeth were primitively small and leaf-shaped. Some derived forms (e.g., diplodocids)

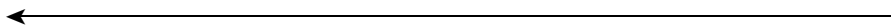


Fig. 15.1 (continued) heterodontosaurids, pachycephalosaurs, basal ceratopsians, and ornithopods, and quadrupedal feeding heights for stegosaurs, ankylosaurs, and derived ceratopsians (ceratopsids). Dashed lines indicate missing data. Herbivorous theropod groups (e.g., Ornithomimosauria, Therizinosauria) are not shown due to space restrictions. Taxonomic abbreviations: AL, *Alamosaurus*; AC, *Acrotholus*; AG, *Agilisaurus*; AN, *Ankylosaurus*; AU, *Auroraceratops*; BA, *Bactrosaurus*; BR, *Brachiosaurus*; CA, *Camptosaurus*; CE, *Cetiosaurus*; CH, *Chaoyangsaurus*; CN, *Centrosaurus*; ED, *Edmontonia*; EO, *Eocursor*; ER, *Europelta*; ET, *Eotrachodon*; EU, *Euhelopus*; FR, *Fruitadens*; FU, *Futalongkosaurus*; GA, *Gargoyleosaurus*; GB, *Gobisaurus*; GO, *Gongxiansaurus*; GR, *Graciliceratops*; GS, *Gastonia*; HA, *Haya*; HE, *Heterodontosaurus*; HN, *Hungarosaurus*; HU, *Huayangosaurus*; HY, *Hypselospinus*; IG, *Iguanodon*; IS, *Isaberrysaura*; JE, *Jeholosaurus*; JI, *Jinzhouosaurus*; KO, *Kotasaurus*; LE, *Leaellynasaura*; LO, *Loricatosaurus*; LU, *Lufengosaurus*; MA, *Mamenchisaurus*; MC, *Macrogyphosaurus*; ME, *Melanorosaurus*; MG, *Magnapaulia*; MI, *Miragaia*; MN, *Manidens*; MO, *Mosaiceratops*; MY, *Mymooropelta*; NE, *Neuquensaurus*; OM, *Omeiosaurus*; OR, *Orodromeus*; OT, *Othnielosaurus*; OU, *Ouranosaurus*; PA, *Panphagia*; PC, *Pachycephalosaur*; PK, *Parksosaurus*; PL, *Plateosaurus*; PR, *Prenocephale*; PS, *Psittacosaurus*; PT, *Patagotitan*; SA, *Sauropelta*; SC, *Scutellosaurus*; SE, *Stenopelix*; SH, *Shantungosaurus*; SP, *Spinophorosaurus*; ST, *Stormbergia*; TA, *Talarurus*; TI, *Tianyulong*; TL, *Talenkauen*; TR, *Triceratops*; WU, *Wuerhosaurus*; YI, *Yinlong*; YU, *Yunnanosaurus*; ZU, *Zuniceratops*. Other abbreviations: Ma, Mega-annum. Silhouette credits: R. Amos, A. Farke, S. Hartman, N. Tamura, M. Taylor, E. Willoughby

had simple, peg-like teeth restricted to the front of the jaws; these would have been mechanically ideal for stripping branches of twigs and leaves (Young et al. 2012). Other contemporaneous sauropods (i.e., camarasaurids) had mouths full of robust, chisel-like teeth capable of delivering higher, sustained bite forces, probably for ingestion of harder foodstuffs (Button et al. 2014). *Nigersaurus taqueti* is distinctive in having an unusually broad, flat muzzle lined with a battery of pencil-like teeth (Serenio et al. 2007). This configuration was almost certainly an adaptation for bulk feeding, low to the ground.

Unfortunately, the ecology of most other sauropods is not so easily discernible. Most problematic has been the use of their long necks, and debate has waged over whether they were held horizontally or more nearly vertically. Proponents of the first view maintain that the cervical articulations prevented the neck from being elevated very much (Stevens and Parrish 2005a, b), that the blood pressure necessary to perfuse the brain, with the neck held in a vertical position, would have been dangerously high (Seymour 2009), or that the neck was mechanically more efficient while in a horizontal posture (Woodruff 2017). Proponents of the second view retort that the cervical vertebrae alone are not good indicators of neck posture in modern taxa (Taylor et al. 2009), that stresses distributed through an upright neck would not have been prohibitive (Christian 2010), and that partitioning of the forest strata would have made ecological sense in sauropod-dominated communities (Bakker 1978) (Fig. 15.1b), as it does among ruminants today (du Toit 1990). The debate is, as yet, unsettled, and the arguments grow increasingly nuanced.

15.1.2 Energetics

Dinosaur energetics are among the most difficult aspects of their biology to glean from the fossil record, but palaeontologists are anything but faint of heart. Although a range of educated assumptions must invariably be made, these serve to constrain interpretations within the realm of possibility. Dinosaur energetics are typically considered from the perspectives of supply and demand. On the supply side, Hummel et al. (2008) investigated the suitability of various Mesozoic (non-angiosperm) plants as sauropod fodder by subjecting samples of related living tissue to in vitro fermentation experiments, using gas production as a measure of metabolizable energy, while also quantifying other nutrients. Horsetails, *Equisetum* spp., proved to be the most nutritious, having high levels of both metabolizable energy and crude protein (the high silica content was likely of little concern to those dinosaurs that relied on gut processing). *Araucaria* spp., *Ginkgo* spp. and *Angiopteris* spp. were also likely dietary staples, whereas cycads, tree ferns, and podocarps proved to be poor sources of energy.

On the demand side, the work of Farlow (1976) and colleagues (Farlow et al. 2010) is instructive. It is possible to bracket the possible energy requirements of dinosaurs via consideration of how those requirements scale with body size in both reptilian ectotherms and mammalian endotherms (birds, although descended from dinosaurs, are likely poor models for dinosaur energetics because their physiology is

fine-tuned to the aerial realm). Thus, a single adult *Brontosaurus excelsus*, weighing 3×10^4 kg, might have needed anywhere from 2×10^4 to 50×10^4 kJ of energy per day, depending on the animal's physiology (Farlow et al. 2010). By combining both supply and demand sides of the model, it is possible to further estimate the population density of *B. excelsus* on a Jurassic landscape, which varies from a few large adults.km⁻² (endotherm model) to a few tens of large adults.km⁻² (ectotherm model). Given that the most diverse sauropod communities of the Jurassic were situated in semi-arid climates at mid-latitudes (Noto and Grossman 2010; Mannion et al. 2011), primary productivity is unlikely to have been very high, and sauropods may have needed to seasonally migrate to find appropriate sustenance. Evidence for such migration, between lowland and upland environments, is preserved as oxygen isotope excursions in tooth enamel (Fricke et al. 2011).

15.1.3 True Dinosaurian Grazers?

In spite of the foregoing discussion, there do exist rare examples of grass-eating in the dinosaur fossil record. The first concerns a report of grass phytoliths found inside coprolites (fossil dung) attributed to Late Cretaceous titanosaurian sauropods from India (Prasad et al. 2005), based on their common association with diagnostic skeletal material. The variety of phytolith morphologies is suggestive of the presence of up to five different grass species, including relatives of modern rices, bamboos, and cool-season grasses. Other phytoliths, found within the same coprolites, are attributable to dicotyledons, conifers, and palms. Variation in phytolith preservation implies that some were purposefully ingested as forage, whereas others (particularly from the rarely preserved palms) were consumed incidentally.

A more recent example (Wu et al. 2017) concerns the discovery of grass phytoliths and silicified epidermis within the purported dental calculus (plaque) of the Early Cretaceous basal hadrosauroid *Equijubus normani* from China. These structures are assigned to Poaceae, based on the short-long cellular patterning and short-cell pairing of the epidermis, and on the equidimensional unlobed and slightly lobed morphologies of the phytoliths.

The presence of grass phytoliths in Cretaceous deposits is somewhat unexpected, as it was long held that these defensive structures evolved in response to later mammal grazing during the Miocene (Strömberg 2004). Could grass phytoliths have evolved in response to dinosaur herbivory instead? It seems unlikely; phytoliths are primarily thought to work by exacerbating tooth wear (Strömberg et al. 2016), which is hardly a concern for reptiles with unlimited tooth replacements, including dinosaurs. In the case of sauropods, these animals are unlikely to have done much oral processing, opting instead for hindgut fermentation (Hummel and Clauss 2011). The dental battery of *Equijubus normani*, and other iguanodontians, may have been well-suited for rending grass, but chance finds of gut and fecal contents in these animals indicates a quite varied diet, including conifer and angiosperm twigs and stems, bark, seeds, leaves, and even crustaceans (Currie et al. 1995;

Tweet et al. 2008; Chin et al. 2017). There is, as yet, no solid evidence that dinosaurs co-evolved with any group of angiosperms (Barrett and Willis 2001; Butler et al. 2009). Rather, grass phytoliths may have evolved in response to predation from the hypsodont gondwanatherian mammals or insects (Prasad et al. 2005).

15.2 Fishes

Laura D. Puk

Herbivorous fishes are found in both marine and freshwater ecosystems but are much more abundant in the marine environment. While in terrestrial ecosystems ‘grazing’ and ‘browsing’ refer to the feeding on monocotyl and dicotyl plants, in marine ecosystems, ‘grazing’ and ‘browsing’ refer to the removal of different kinds of algae (Green and Bellwood 2009). Marine grazing fishes remove small filamentous turf algae and marine browsing fishes remove larger macroalgae (Green and Bellwood 2009). In contrast to terrestrial ecosystems, ‘real’ grazing on angiosperms is rare and restricted to only one plant group: seagrasses (Beer 1989). In freshwater ecosystems the terminology is different yet again. The term ‘grazer’ is used for both plant—(‘macrophytes’; Fowler and Robson 1978) and algal—(‘periphyton’, Power 1983) removing fishes, whereas the term ‘browser’ is not used at all.

Where a distinction between grazing and browsing fishes is made, they are faced with different challenges in terms of intake and digestion of their respective food source. Grazers feeding on turf algae ingest a low energy but relatively easily digestible and abundant resource. Browsers feeding on macroalgae on the other hand are faced with a resource that provides more energy, but exhibits chemical and structural defences, is difficult to digest, and patchily distributed. Both groups exhibit adaptations to their respective resources, including differing home range sizes (Nash et al. 2013; Welsh and Bellwood 2014), bite rates (Randall 1967; Burkepile and Hay 2010), and digestive mechanisms (Clements et al. 2009). Browsers are often larger in body size than grazers, potentially enabling them to take bigger, stronger bites (Bonaldo and Bellwood 2008; Lokrantz et al. 2008). They also have larger home ranges (Nash et al. 2013), which helps them locate their food and they take less frequent bites (Cardoso et al. 2009; Burkepile and Hay 2010), because their resource is more energy-dense. After ingestion, browsing fishes utilise fermentation to break down the macroalgal cell walls to access the nutrients (Clements et al. 2009); a mechanism not required by grazers.

While the importance of herbivorous fishes in marine ecosystems has been recognized for a long time, research in freshwater systems mainly focused on insects (Lodge et al. 1998) but is now recognizing the impact of herbivorous fishes on macrophytes (Lodge 1991; Lodge et al. 1998). Herbivorous fishes hold crucial functions in both freshwater and in marine systems, albeit of a different nature. In freshwater systems, they contribute significantly to seed dispersal in seasonally flooded forest ecosystems (Anderson et al. 2011; Horn et al. 2011), exhibiting

some of the longest dispersal distances discovered in animals, including African hornbills and Asian elephants (Anderson et al. 2011). However, due to their removal of macrophytes, they can increase phytoplankton biomass and shift lakes towards a turbid state if certain conditions are met (Van Donk and Otte 1996). Grazing and browsing fishes exhibit their highest diversity in marine ecosystems, especially on coral reefs (Gaines and Lubchenco 1982), which has led to a research focus on these ecosystems. Here, herbivorous fishes are considered to provide a key ecosystem function because they control algae, which compete with the primary reef builder—corals.

On coral reefs, herbivorous fishes can consume up to 90% of the primary production (Carpenter 1986; Polunin and Klumpp 1992) and, therefore, play a major role in controlling the reef state. Grazers are more abundant than browsers (Choat et al. 2004), and coupled with their higher feeding rates (Burkepile and Hay 2010), they are responsible for consuming most of the primary production (Burkepile and Hay 2010). Coral reefs dominated by corals are considered ‘healthy’, but if grazing pressure is reduced, they often become dominated by algae (Hughes et al. 2007; Webster et al. 2015). Grazing pressure can be reduced due to overfishing, which is simulated experimentally by excluding fishes with cages (Bellwood et al. 2006; Webster et al. 2015), or due to coral bleaching events which kill vast amounts of corals, freeing up space for algal settlement (Hoegh-Guldberg 1999). Sudden increased availability of space reduces the grazing pressure per unit area on a reef (Williams et al. 2001; Mumby et al. 2007; Mumby 2009), because the existing fish community now has to distribute its feeding activity over the additional free substrate. Once a reef is dominated by algae a return to a coral-dominated state is difficult as macroalgae inhibit coral recruitment (Kuffner et al. 2006; Webster et al. 2015) and survival (Box and Mumby 2007; Webster et al. 2015). Algal-dominated reefs provide less ecosystem services to people compared to their healthy coral-dominated counterparts (Moberg and Folke 1999).

Shifts to algal-dominated coral reefs are projected to increase in the future due to climate change (Hoegh-Guldberg 1999). Higher temperatures cause a higher frequency of coral bleaching events and subsequent mass coral mortality (Hoegh-Guldberg 1999; Hughes et al. 2018). Additionally, algae experience a net positive physiological effect with rising temperatures, whereas corals experience a net negative physiological effect (Elfwing and Tedengren 2000). This could shift the competitive interaction further in favour of algae. However, grazing intensity is greater at higher temperatures (Smith 2008) and may counteract the increased primary production (O’Connor 2009). Higher production and herbivory can strengthen the producer-consumer interaction (O’Connor 2009) which may become a feature of future ecosystems. A strengthening of this interaction could increase the importance of herbivorous fish for the health of consumer-dominated ecosystems such as coral reefs even further.

While the state of coral reefs is heavily controlled by herbivorous consumers, other ecosystems are less dependent on consumers and instead producer-dominated (Connell et al. 2011). One example are kelp forests, common temperate marine ecosystems, where native herbivores (mostly invertebrates such as sea urchins)

exhibit only minor control over the ecosystem state (Connell et al. 2011). However, rising temperatures cause a range expansion of tropical herbivorous fishes, which could have detrimental effects on kelp forests (Vergés et al. 2014). After a kelp die-off in Western Australia, tropical browsing fish (kyphosids) that had moved into higher latitudes consumed kelp and created a new barren ecosystem state dominated by turf algae (Bennett et al. 2015). Herbivorous fishes may, therefore, shift the production-dominated temperate marine systems towards consumption-dominated alternative states (Bennett et al. 2015). The strengthening of the producer-consumer interaction (O'Connor 2009), and the switch from production-dominated to consumer-dominated temperate systems (Bennett et al. 2015), suggest a stronger influence of grazers and browsers on future marine ecosystems. Only time will tell.

Similarly strong changes may occur in freshwater ecosystems. Increased grazing, for example through higher metabolic rates associated with increased temperatures, could destabilize the clear-water macrophyte-rich state of lakes and shift them to a phytoplankton-dominated turbid state (Van Donk and Otte 1996). Additionally, increased frequencies of droughts may decrease the number or intensity of floods in forest ecosystems that experience substantial seed dispersal by fishes (Horn et al. 2011). This could decrease the dispersal of plants, especially upstream (Horn et al. 2011). Overfishing can further intensify the problem as bigger fish are often targeted first but they are also the most effective long-distance dispersers (Anderson et al. 2011). Whether the role of fish as a disperser is important enough to make their disappearance noticeable in the forest community structure is currently unknown.

The potentially significant future ecosystem changes connected to herbivorous fishes highlight the importance of understanding their ecosystem function in detail. The study of the role of browsing and grazing fishes is still in its infancy and there is a lot to be learnt from studies on terrestrial ecosystems. However, fish herbivory is likely to differ from terrestrial herbivory because producers and consumers are structurally and functionally distinct from their terrestrial counterparts. Research should focus on understanding the drivers of food choice in herbivorous fishes, how climate change and habitat degradation influence interactions between herbivores and their ecosystems, and identify potential feedbacks.

15.3 Reptiles

Everton B. P. Miranda and Carolina Starling-Manne

Among reptiles, lizards and chelonians are the only modern groups that strictly, or mostly, feed on plant-matter (King 1996). Snakes are obligate carnivores, and crocodiles have evolved herbivory habits a few times in their evolutionary history (Kley et al. 2010; Fiorelli et al. 2016), but there is no modern herbivorous crocodile species. However, a large diversity of chelonian and lizard species is adapted to feed on plants, with several insular radiations that represent most of this diversity.

Given the physiological demands of digesting cellulose and high-fibre plant material, reptile species specialized for grazing and browsing are typically large-sized tropical or sub-tropical species (Pough 1973; Cooper and Vitt 2002; but see Espinoza et al. 2004). The latitude constraint is caused by temperature-dependent limitations to fermentation rates by bacteria in the gut, which require high temperatures to perform their activities (Cooper and Vitt 2002). Being ectotherms, reptiles do not maintain their body temperature stable, and would likely lose their microbial symbionts over cold winters, so full herbivore reptiles are usually restricted to tropical and subtropical climates. In terms of size, large ectotherms become two to three times smaller per each 10 °C of decrease in ambient temperature (Makarieva et al. 2005), due to metabolic constraints. There is also the need of having enough space to allow the fermentation of large amounts of fibre and cellulose (Pough 1973), so herbivory in ectotherms usually requires a large body size.

Consequently, many of the largest continental species of reptiles, and the megafauna in islands, are herbivorous lizards and chelonians (Hansen and Galetti 2009). Martin (1984) defined megafauna as animals above 44 kg, but throughout this section we will be using an operational concept of megafauna, which is animals whose evolution is constrained by the size of the land area each species inhabits (Burness et al. 2001; Hansen and Galetti 2009). Also, it is worth noting that reptiles are the vertebrates that achieve some of the highest densities and biomasses in terrestrial ecosystems, reaching up to around 600 kg.ha⁻¹ (Arce-Nazario and Carlo 2012; Lovich et al. 2018; Fig. 15.2). Since the grazing and browsing pressure of an herbivore is magnified by its density and biomass, in some ecosystems the ecological role of reptiles is also magnified.

15.3.1 Diversity

15.3.1.1 Insular

Some of the most conspicuous kinds of grazing and browsing reptiles are giant insular tortoises and iguanas (Gerlach 2014; Hastings et al. 2014). The colonization restrictions of islands normally results in a “reptile-only” megafauna (Hansen and Galetti 2009). In these ecosystems, tortoises have evolved, on multiple occasions, domed shells when grazing over grasslands and craning necks and saddleback shells when browsing over trees, shrubs, cacti, and palms. In the past, giant tortoises inhabited climates ranging from mediterranean to tropical climates, including archipelagos in the Mediterranean sea, and the Caribbean, Indic and Pacific oceans (Turtle Extinctions Working Group 2015). Today, there are extant island giant tortoise populations of only two species complexes, in the Galápagos Islands (*Chelonoidis niger* spp.) and in the Seychelles Islands (*Aldabracheys gigantea*; Hansen et al. 2010).

Another group of browsing and grazing reptiles are iguanas (Cooper and Vitt 2002). They represent a diverse group (Uetz et al. 2016), with three insular radiative adaptations in the Caribbean (nine species in the *Cyclura* genus), the islands of Fiji



Fig. 15.2 Densely packed green iguana (*Iguana iguana*) populations occur across a wide area of Neotropical forests. In this photo, several adult males display during the breeding season. <http://www.thinkstockphotos.ca/image/stock-photo-iguanas-in-a-tree-in-mexico/464974882>

and Tonga (six species in the *Brachylophus* and *Lapitiguana* genus, from which the two largest species are extinct), and the Galápagos archipelago (three terrestrial species from the *Conolophus* genus). As is the case with their continental counterparts, insular iguanas are mainly browsers, also being important for seed dispersal (Laurel et al. 2000; Meehan et al. 2002; Traveset et al. 2016). To complete the list, two other insular browsers are the monkey tailed lizard, *Corucia zebrata*, from the Solomon Islands, and the lacertid lizards, *Galotia* spp., from Mediterranean islands (Espinoza et al. 2004).

15.3.1.2 Continental

Continental browsing by lizards is restricted to iguanids in the Neotropics, such as the widespread green iguana, *Iguana iguana*, and by other species that are not so specialized on leaf or grass material, such as *Ctenosaurus*, *Sauromalus*, and *Dipsosaurus* (Vitt and Caldwell 2013). The only significant species outside the Neotropics are the mostly-grazing desert-specialists in the genus *Uromastyx* (Wilms et al. 2010), and the partial-browsers of the genus *Hydrosaurus*.

Large continental grazing chelonians (heavier than 44 kg) used to be found on all continents apart from Antarctica. As with most of the megafauna, they are now extinct in most of their historical range, except for the African continent (Martin 1984; Turtle Extinctions Working Group 2015). For herbivorous reptiles, the extinctions were caused mainly by direct and indirect effects of human action, including

over-exploitation, and pressures exerted by invasive species (Turtle Extinctions Working Group 2015; Slavenko et al. 2016). Large continental grazing tortoises can only be found today in Africa (Turtle Extinctions Working Group 2015), likely due to their history of co-existence with hominids (Klein 1984). There are two widely known species of tortoises that fit this role, the leopard tortoise, *Stygmochelis pardalis*, and the spurred tortoise, *Centrochelys sulcata*. While the former may weigh up to 48 kg, and feeds almost exclusively on grasses (Branch et al. 1990), spurred tortoises are truly specialized grazers, that weight up to 96 kg (Lambert 1993), and are the last representatives of giant grazing tortoises on continental ecosystems. A few other smaller grazing tortoise species still inhabit continents, such as the Bolson tortoise, *Gopherus flavomarginatus*, from Mexico, the yellow-footed tortoise, *Chelonoidis denticulatus*, from South America and the Asian forest tortoise, *Manouria emys*, from Southeast Asia. Among the extinct giant species of continental tortoises are the *Chelonoidis lutzae* in South America, *Hesperotestudo* spp. in North America, Meiolanids (horned turtles) in Australia and the *Megalochelys* spp. in Asia (estimated weight: 1000 kg; Badam 1981)—being the latter the largest tortoises to have ever lived (Turtle Extinctions Working Group 2015).

15.3.1.3 Marine

Green sea turtles, *Chelonia mydas*, play a conspicuous role as a marine grazer, paralleling grazing ungulates in many aspects of their ecology (Christianen et al. 2014). They have some degree of endothermy which allows them to graze on water temperatures around 20 °C (Heath and McGinnis 1980). Furthermore, two species of herbivorous reptiles are known as being associated with marine habitats. First, there is the marine iguana from the Galápagos Islands, which is a grazer, feeding on the rocky subtidal and intertidal zones of the archipelago (Shepherd and Hawkes 2005). Marine iguanas have tight schedules of basking and foraging—the second being usually restricted to only 1 h a day—which allows them to graze on the cold Galapagos waters. A second species, closely associated to marine ecosystems, is *Ctenosaura bakeri* (Köhler 2004), a browsing iguana, endemic to the mangroves of the Utila Island, in Honduras, in the Caribbean.

15.3.2 Effects on Vegetation Composition and Dynamics

Giant tortoises are highly influential on both insular and continental ecosystems, being best known as important seed dispersers (Falcon et al. 2018). They also play the, perhaps less appreciated, role of grazers and browsers on vegetation, affecting vegetation community composition and structure (Lovich et al. 2018).

Grazing herds of giant tortoises reportedly create and maintain a grassland ecosystem called tortoise turf on islands in the Indian Ocean (Gibson and Hamilton

1983; Cheke and Hume 2010). Composed of grasses, sedges and herbs, tortoise turf occurs in areas of high-tortoise concentration and, therefore, heavy grazing. Many of its characteristic plant species are dwarfs with highly specialized growth strategies (e.g., flowers and fruits produced at the base of the plants; Merton et al. 1976). This is a dominant ecosystem in the Seychelles and used to be widespread at the Mascarene Islands (Cheke and Hume 2010; Griffiths et al. 2010). Tortoise terraforming is, in its turn, important to other insular species of plants and animals (Griffiths et al. 2010, 2011, 2013). Many plants in the Mascarene archipelago have two kinds of foliage, from which their low-hanging leaves have adaptations to lower or no levels of herbivory by tortoises (Eskildsen et al. 2004). This phenomenon illustrates the high grazing pressure that can be exerted by large herds of tortoises. Tortoise-exclusion experiments are in operation on Aldabra, and are likely to show the importance of these keystone herbivores on the archipelago's vegetation dynamics in the near future. On the other hand, on some islands, where native giant tortoises have been extirpated, similar-species tortoise introductions are being conducted, as ecological replacements to restore important lost ecosystem functions. For example, that approach is rebuilding trophic interactions (e.g., herbivory and seed dispersal networks) on some islands of the Mascarene archipelago (Griffiths et al. 2010, 2013).

On the Galápagos Islands, giant tortoises are known to maintain plant communities with an upper strata, formed by arborescent cacti (Gibbs et al. 2010). If tortoises have been extirpated, these plant communities become encroached by woody vegetation (Hunter and Gibbs 2014). The Anthropocene extinctions, translocations and population fluctuations of tortoises in the Galapagos archipelago provided many ecological quasi-experiments to test the effects of these ecosystem engineers (Gibbs et al. 2008; Froyd et al. 2014). Tortoise reintroductions, after decades of absence, cause a marked rebuilding of cactus population, reducing clustering and increasing juvenile cactus recruitment (Gibbs et al. 2010). Intense grazing, soil disturbance, browsing, seed dispersal, pool forming and direct vegetation damage are some of the means by which giant tortoises restore degraded ecosystems in the Galápagos (Hamann 1993; Blake et al. 2012, 2013; Froyd et al. 2014).

The effects of grazing and browsing on vegetation composition and dynamics, by continental tortoise species, are still largely uninvestigated (Falcon et al. 2018). The last representative of giant tortoises in continental ecosystems, the spurred tortoise, is threatened by extinction in the wild, mainly due to collection for the pet trade and the bush meat industry (Garrigues and Cadi 2011; Petrozzi et al. 2018). The ecological effects of the removal of a potential ecosystem engineer are poorly understood. The same problem of lack of vegetation impact studies occurs with other large-sized tortoise species, such as the yellow-footed tortoise (up to 54 kg), the leopard tortoise (up to 48 kg) and the Asian forest tortoise (up to 37 kg). Hopefully, the reintroductions planned for some of those species will mirror the ecological quasi-experiments in Galápagos and in the Mascarenes. Thereby, we would gain invaluable insight into the ecological roles of the last representatives of large tortoises on continental vegetation dynamics, other than as seed dispersers.

Whereas there are many excellent studies on the foraging behavior of iguanids, studies of their role on vegetation dynamics have mainly focused on seed dispersal (Valido and Olesen 2007). As with tortoises, many iguanas play an important role increasing the germination rate and decreasing the germination time of several angiosperm species, some of the plants also threatened (Traveset 1990; Laurel et al. 2000; Moura et al. 2015; Traveset et al. 2016). The smaller size of iguanas, and their low metabolism (averaging just $\sim 70 \text{ kcal}\cdot\text{day}^{-1}\cdot\text{kg}^{-1}$ for *Iguana iguana*; Lichtenbelt 1992), suggest they may influence vegetation dynamics through browsing and grazing to a lesser degree than do tortoises. However, by attaining extremely high densities, in both continental and insular ecosystems (up to $364 \text{ ind}\cdot\text{ha}^{-1}$ in continental *Iguana iguana*; Rodda 1992), and by browsing or grazing over a small home range (Moura et al. 2015), they may be able to affect vegetation composition by: i.) reducing the leaf area of browsed species; ii.) increasing the amount of sunlight that reaches the undergrowth; and, iii.) affecting edaphic mosaics in the soil, by the repeated deposition of feces in latrines. It is hoped that these research gaps will be addressed in the future.

Marine, grazing reptiles, such as marine iguanas and green turtles, feed mostly on algae. Marine iguanas forage non-selectively on subtidal and intertidal zones, choosing abundant red and green algae species and avoiding brown algae (Shepherd and Hawkes 2005). While each adult consumes a fresh mass of just 35 g of algae per day, they can reach high densities, so populations of marine iguanas can crop a sizeable amount of fresh algal material (27–29 tons yearly for a single population in a 3 km^2 peninsula on the Galápagos Islands; Nagy and Shoemaker 1984). Together with decreased water temperature, during El Niño years, population numbers of marine iguanas are often limited by bottom-up effects on the algae cover of rocky substrata (Wikelski and Thom 2000). Green turtles, the only other herbivorous marine reptile, also feed almost exclusively on algae and sea grass. They prefer low-fibre and high nitrogen species, mainly *Thalassia* spp. (turtle grasses), although all algae grazed by green turtles are low-quality forage (Bjorndal 1980). Sea turtles graze on algae and sea grasses, keeping them fertilized with their dung (Moran and Bjorndal 2005; Hearne et al. 2018). Sea turtles further parallel the terrestrial ungulates by having complex space use relationships with their predators. The food resource of turtles could be at risk under conditions that their natural predators, namely sharks, are rare or absent due to overfishing (Heithaus et al. 2014).

15.3.3 Direct Impact of Domestic Herbivores

Habitat destruction resulting from introduced ungulates is a classical threat to grazing and browsing reptiles (Fig. 15.3). The transformation of forest ecosystems into grasslands, or the poor management of ungulates in natural grasslands, continue to negatively affect grazing and browsing reptiles all over the world. *Uromastix* lizards—important ecosystem engineers (Williams et al. 1999)—are negatively impacted by heavy grazing pressure imposed by livestock (Cunningham 2000).



Fig. 15.3 A grassland grazed by introduced cattle on Santa Cruz Island, in Galápagos. In this photo, a cow and a giant tortoise, *Chelonoidis porteri*, share a field. <https://www.alamy.com/stock-photo-wild-galapagos-giant-tortoise-geochelone-elephantopus-with-cow-on-164775731.html>

Other grazing species, such as the tortoises of the genus *Gopherus* and the spurred tortoise, are also negatively affected by competition for forage resources with cattle, *Bos taurus*, (Grandmaison et al. 2010; Ureña-Aranda et al. 2015; Becerra-López et al. 2017; Petrozzi et al. 2018). Also, habitat loss in the form of forest fires, set by cattle-ranchers in tropical ecosystems, are frequent all over the world (Gibbons 1984; Wiewandt and García 2000; García and Gerber 2016; Tershy et al. 2016). Direct ecosystem conversion for beef and dairy cattle production is bound to continue (Fearnside 2018), whereas the harvest of native species (including reptiles), for food, remains largely unmanaged, unsustainable and irresponsible in most tropical countries (Fa et al. 2002; Fernandez et al. 2012; Terborgh and Peres 2017).

15.4 Concluding Remarks and Further Developments

Rather than biological oddities, large-sized herbivorous reptiles are fundamental components of some vertebrate communities of tropical and subtropical environments, all over the world (Miranda 2017). The low metabolic rate of reptiles allows them to exist at extremely high biomasses, as testified by early naturalists (Von Humboldt 1877; Leguat 2017), or in ecosystems that have not yet been destroyed by humans (Bourn et al. 1999; Mourão et al. 2000). Many of these important species

have disappeared, with a higher rate of extinction for giant lizards and tortoises (Turtle Extinctions Working Group 2015; Slavenko et al. 2016). Ecological networks have been impoverished by the loss of these large herbivores, likely resulting in simpler, shorter and less resilient trophic networks (Malhia et al. 2016). For the remaining herbivorous reptilian species, their direct impacts on vegetation dynamics are still being discovered. Results coming from natural and planned ecological quasi-experiments on islands show the importance of large herbivorous reptiles for ecosystem composition, structure and function (Gibbs et al. 2010; Griffiths et al. 2013). Another interesting research avenue, yet to be explored, is investigating the role reptilian aquatic herbivores play for the ecosystems in which they exist. Some freshwater turtles, such as the Amazon giant river turtle, *Podocnemis expansa* (up to 65 kg), and the Central American river turtle, *Dermatemys mawii* (up to 22 kg), feed mostly on leaves. These species are seasonal or year-round browsers, and hold the potential to exert pressure on the submerged arboreal vegetation, and act as links between terrestrial and aquatic ecosystems.

Finally, the last decade has seen a multitude of translocation programs targeting threatened tortoises, turtles, and herbivorous lizards (Jones 2002; Attum et al. 2010; Nussear et al. 2012; Gibbs et al. 2014; Grant and Hudson 2015; Falcón and Hansen 2018). These conservation initiatives have been restoring not only threatened species populations, but also lost or diminished ecological interactions. Knowledge about the effects of those translocations on the vegetation dynamics of continental floras will provide information on rebuilding reptile-driven ecological interactions (*sensu* Genes et al. 2017) such as trampling, seed dispersal, grazing and browsing. While considered by many as “primitive” and dull, reptiles are significant players in the ecosystems they inhabit, and perform important functions as predators, pollinators, burrowers and frugivores. Acquiring knowledge on their role as grazers and browsers is a promising ecological research venture.

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15.5 Birds

René van der Wal

15.5.1 *Grazing and Browsing Birds*

Foraging on plants is very widespread among birds. The most common form this takes is the selection of high energy and nutrient forage item such as seeds and fruits. Quite a number of species have specialised in this foraging strategy (see Whelan et al. 2015 for impacts of granivorous and frugivorous birds on ecosystems), but many more take these items as part of a much broader—often omnivorous—diet. Far fewer have adopted grazing or browsing as their main mode of foraging (see Lopes et al. 2016 for a classification of avian diet types), estimated to be the case for 101 species (80 grazers and 21 browsers—Table 15.1), and thus less than 1% of the World's extant bird species (9993—Jetz et al. 2012). The distribution of herbivorous birds is strongly skewed towards a single phylogenetic order and family therein, namely the Anatidae or ducks, geese and swans (Table 15.1). All swans and geese

Table 15.1 Orders and families with bird species for which grazing or browsing is the main mode of foraging. The number of species per family that is primary grazing or browsing was estimated using <https://en.wikipedia.org/wiki/aves> and <https://globalspecies.org/ntaxa/114863> as starting points, and consulting additional secondary sources (e.g., various Cornell Lab or Ornithology resources, Handbook of the Birds of the World <https://www.hbw.com>) or primary sources for further information or triangulation where information was insufficient. Phylogeny is after Jarvis et al. (2014)

Order	Family	Species (groups)	Primarily grazer	Primarily browser
Struthioniformes	Struthionidae	Ostriches	2	
Rheiformes	Rheidae	Rheas	2	
Cassuariiformes	Dromaiidae	Emu	1	
Anseriformes	Anseranatidae	Maggie goose	1	
	Anatidae	Ducks, geese and swans	51	
	Anhimidae	Screamers	3	
Galliformes	Phasianidae	Grouse		17
Opisthocomiformes	Opisthomidae	Hoatzin		1
Gruiformes	Gruidae	Cranes	6	
	Rallidae	Coots, moorhens	12	
Columbiformes	Columbidae	Pigeons and doves	1	
Psittaciformes	Strigopidae	Kakapo	1	
Passeriformes	Cotingidae	Plantcutters		3
Total number of species			80	21

are obligate herbivores, although occasionally consuming other food items too (e.g., insects, bones or even soil—Abrahams 2013). The extent to which plant-eating ducks consume plant material (other than seeds) varies considerably among species and the time of the year (Olsen 2015). About 20 ducks (e.g., whistling ducks, some diving ducks including pochards, and several dabbling ducks including wigeons, gadwall, *Anas strepera*, and Australian wood duck, *Chenonetta jubata*, can be considered primarily herbivorous, for at least part of the year (Table 15.1), but all will shift towards a more omnivorous diet during spring and summer to meet protein requirements for breeding and growth (Sedinger 1997).

Whilst many of the above Anatidae also consume seeds when present (and thus are in part, and to a various extent, also granivorous), grazing of grasses, sedges and forbs is the predominant mode of foraging. Grazing typically concerns the consumption of aboveground tissue of non-woody plants (notably leaves but also stems and seed heads, the latter particularly in the case of agricultural crops), but this regularly spills over in the extraction of belowground plant organs such as tubers and rhizomes (Fox and Abraham 2017). For some species groups, shorter or longer periods of the year are dedicated to such foraging for energy-rich storage organs—captured by the term ‘grubbing’ (Anderson et al. 2012)—which requires considerable strength, and hence is typically conducted by larger species (e.g., ostrich, cranes, larger-bodied geese, swans; Zhiheng and Clarke 2016). Several other aquatic families, or members thereof, such as screamers, coots and some moorhens, are primarily grazers—or consumers of belowground plant parts—too, as are several flightless members of the phylogenetically oldest clade (Palaeognathae) of extant birds (emu, *Dromaius novaehollandiae*, rheas), the common wood pigeon, *Columba palumbus*, and the large, flightless, and critically-endangered kakapo, *Strigops habroptilus*, whose diet (e.g., clubmosses, ferns and bark, and thus leaning towards being a browser—Best 1984) is as unusual as its appearance. Many more bird species consume fresh green shoots, flowers and buds (e.g., pheasants, turkeys, rails, turacos), or extract rhizomes, roots and bulbs (e.g., bustards, sandgrouse, tinamous), but only in limited amounts, and at certain times of the year, and are thus not genuine grazers.

Grouse is the family of birds with most genuine browsers (all 17 species—Table 15.1), often almost exclusively living from shrubs, or tree leaves and needles, outside the breeding season. Many also consume seeds, with the exception of the two sage-grouse, which lack a muscular gizzard and, therefore, consume only soft-tissue foods (mainly leaves of sagebrush). Within the breeding season, grouse diets are generally enriched with invertebrates (Sedinger 1997). Other bird species that forage primarily on buds, leaves and twigs are the three plantcutter—the only folivorous passerines (Bucher et al. 2003)—and the Amazonian-dwelling hoatzin, *Ophithocomus hoazin*. The latter has even developed a crop and oesophagus with fermentation functionality akin to rumen-digestion (Grajal et al. 1989; Godoy-Vitorino et al. 2011).

With the exception of the Rattites (large flightless birds including ostriches, rheas and emu) and the (poorly flying) hoatzin—both of which can digest cellulose (Swart et al. 1993; Grajal et al. 1989)—the requirement to fly has prevented birds from

developing relatively heavy but efficient digestive systems to deal with e.g., plant material (Caviedes-Vidal et al. 2007; but see Hunt et al. 2019 for limited evidence between flying ability and caecal length—greatest for grazers—within birds). This has two important consequences: firstly, a limited ability to digest cellulose and other highly recalcitrant plant parts (Prop and Vulink 1992; Durant 2003), meaning that large amounts of plant material need to be consumed; secondly, there is an even greater premium on plant quality than is the case for most other herbivores, as selection of the most nutritious and/or energy rich (depending on requirements and time of the year) food items—in itself a time-consuming process—is the only way to maximise daily nutrient and/or energy gains. Combined, many herbivorous birds have to forage for most of the day (Prop and Vulink 1992). For grazers, having to use a bill as feeding device brings the additional constraint of reduced bite size as compared to mammalian grazers. This may, in part, be compensated for by employing a greater bite frequency in order to achieve comparable instantaneous food intake rates (Steuer et al. 2015), or require further adaptation, in the form of yet longer daily foraging times (Van Gils et al. 2007). This puts in sharp focus the trade-off between plant quantity and quality, and with it a set of key behavioural adaptations (see below) to try and achieve the highest possible intake rates of high quality food items. Whilst none of these adaptations is unique to birds, and indeed trade-offs between quantity and quality rule foraging decisions of all herbivores (and beyond), birds' limited digestive ability of plant material tends to make conditions more extreme.

15.5.2 Ecosystem Impacts of Grazing and Browsing Birds

Many of the ecosystem impacts of birds observed today could be understood in the context of digestive constraints on herbivorous birds, whereby the ability to i) aggregate into groups to optimise foraging time and food finding (Stahl et al. 2001; Gyimes et al. 2010; Kułakowska et al. 2014); ii) undergo carefully scheduled movement and migration, to and from a limited number of sites, and thus requiring individuals, in a number of herbivorous bird species, to make decisions at larger spatial and temporal scales (Arzel et al. 2006; Van der Graaf et al. 2006; Shariatinajabadi et al. 2014); and, iii) seek out, and subsequently utilise, new 'high quality' foraging opportunities (Van Eerden et al. 2005; Si et al. 2015; Fox and Madsen 2017; Buij et al. 2017), are key behavioural adaptations to those constraints.

For grazing or browsing birds, to exert large-scale impact on the vegetation, species need to be abundant and use a location for a reasonable length of time. As a consequence, herbivorous birds that are gregarious tend to have greatest impact on the ecosystems they inhabit (Wood et al. 2012; Kollars et al. 2017), though exceptions occur (e.g., ptarmigan controlling shrub architecture—Tape et al. 2010). Large aggregations concern mostly—but not exclusively (e.g., coots, cranes, wood pigeons)—“waterfowl”, a loosely defined label that typically concerns ducks,

geese and swans, and sometimes also rails. As the label suggests, waterfowl use both terrestrial and aquatic ecosystem components, and impacts on land are often inextricably connected to those occurring in nearby freshwater, or marine, ecosystems and vice versa (Hessen et al. 2017; Kollars et al. 2017).

15.5.3 Bird Density and Existence of Plant Refuge Determine Marine Ecosystem Impact

Impacts on marine ecosystems are restricted to the intertidal or shallow subtidal, and those zones are typically used seasonally, coinciding with spring or autumn migrations. For example, beds of seagrass, *Zostera spp.*, are in high demand by brent geese, *Branta bernicla*, black swan, *Cygnus atratus*, mute swan, *Cygnus olor*, and American wigeon, *Anas americana*, but *Zostera* also occurs frequent in the diet of a further 20 waterfowl species (Kollars et al. 2017). Consumption of both above- and belowground components may severely reduce seagrass abundance, though accumulation of seeds in feeding pits, in autumn, can facilitate seedling recruitment in spring, thereby contributing to the persistence of seagrass beds (Zipperle et al. 2010). In some areas waterfowl may control the abundance and distribution of seagrasses (Kollars et al. 2017), in other areas (e.g., Gulf of Mexico where redhead duck, *Aythya americana*, forages extensive on seagrass beds that represent economically important fish nursing habitat—Kennedy et al. 2018), impacts appear to be limited. Critical to the extent of bird herbivory impact, in shallow marine, as well as comparable freshwater, systems (e.g., swans foraging on pondweeds, *Potamogeton spp.*—Klaasen and Nolet 2007), is not only the density of birds, and duration of resource use, but also the existence of spatial refuges for plants (e.g., belowground plant parts that are out of reach—Santamaria and Rodríguez-Gironés 2008), and safe sites for seedling establishment to ensure plant regrowth and recruitment. Although recovery of previously endangered waterfowl, due to successful conservation efforts, combined with ongoing expansion of already highly successful species, may exert further impact on seagrass beds (Kollars et al. 2017), the attraction of most *Zostera*-consuming species to agricultural land for foraging (Fox and Madsen 2017) is likely to mitigate against greater bird grazing impacts on marine ecosystems.

15.5.4 Expanding Waterfowl Populations Contribute to Top-Down Control of Freshwater Ecosystems

The impacts of ducks, geese, swans and rails on freshwater ecosystems are manifold, but key are the accumulation of nutrients, bio-turbidity and the consumption of macrophytes (Wood et al. 2012; Bakker et al. 2018). A further significant, although

less directly observable, impact, is the contribution by waterfowl to wetland biodiversity around the world, through the transport of a wide variety of aquatic plants and animals between wetlands and water bodies (Van Leeuwen et al. 2012). Extensive consumption of water plants, in lakes, by birds, does occur, but in most cases this is limited to very shallow, and often heavily vegetated, systems (e.g., swamps), although ponds may also be subject to intense waterfowl herbivory (and indeed kept apparently free of vegetation—Van Onsem and Triest (2018)). Within deeper lakes, there may be brief episodes of heavy grazing, for example when large numbers of waterfowl gather to moult during which they are flightless, and hence prone to predation (e.g., moult migration by greylag geese, *Anser anser*—Zijlstra et al. 1991). Whereas 3 decades ago, recognition of waterfowl shaping freshwater ecosystems, beyond single sites, was limited, the rapid increase in waterfowl abundance in recent years has changed this. In a review, Bakker et al. (2018) concluded that, currently, herbivorous birds remove 40–48% of plant biomass in aquatic ecosystems, well in excess of exploitation levels found in most terrestrial ecosystems. Impacts are manifold with, for example, the dramatic expansions of greylag geese being held responsible for the decline in reed, *Phragmites europaeus*, beds across Europe (Bakker et al. 2018), with knock-on effects on numerous species of insects and breeding birds. Moreover, the accumulation of nutrients, deposited in the water as uric acid and faeces, in no small part originating from food plant consumed in the terrestrial realm, is now viewed as default, and increasingly the main eutrophication agent in lakes and ponds (Chaichana et al. 2010; Hessen et al. 2017). Whilst there is strong evidence for birds causing eutrophication, bioturbation and the reduction of aquatic plant abundance, and for bird density to be related to the extent of plant biomass suppression, this is also the case for other species groups (e.g., mammals, crustaceans, molluscs, fish, echinoderms—Wood et al. 2016 and elsewhere in this Chapter and Book). Hence, the current, and likely further, increasing impacts of herbivorous birds on freshwater ecosystems may best be viewed as contributing to a wider top-down control of primary productivity. It is likely that only part of the complexity of herbivorous bird impact on freshwater ecosystems has been revealed because of the large number of species interactions and mechanisms involved (e.g., influence of carp on habitat choice of water birds—Haas et al. 2007). Whilst the impact of birds on macrophytes, in water bodies, is thus beyond doubt, its impact on rivers is still deemed limited, and mostly local (Franklin et al. 2008).

15.5.5 Agriculture Drives Grazing Bird Abundance and Terrestrial Ecosystem Impacts

Numerous studies have revealed the intricate nature of impacts exerted by grazing and browsing birds on terrestrial ecosystems. Key to large-scale herbivore impacts are changes in wider land use, government policy and climate which, collectively, have allowed, notably waterfowl, to greatly increase in abundance (e.g., Jefferies

et al. 2004; Van Eerden et al. 2005). Long-term changes in the quality of the vegetation on offer in grasslands and arable lands have, together with reductions in hunting practice and the formation of nature reserves, driven down over-winter mortality of waterfowl (Fox and Madsen 2017). Particularly dramatic population expansions have occurred in arctic-breeding geese, raising the status of e.g., the lesser snow goose, *Chen caerulescens*, to one of the world's most abundant grazing birds. The impact of this species on their breeding grounds has been evidenced particularly well in and around La Pérouse Bay, Hudson Bay area, subarctic Canada. Here, the relationship between snow geese and the subarctic tundra vegetation changed from one characterised by finely tuned herbivore-plant-soil feedbacks, which allowed geese to optimise food intake (Hik and Jefferies 1990), to a situation in which extensive loss in vegetation cover occurred, due to grubbing. The dramatic increase in the number of breeding and spring-staging lesser snow geese, together with a comparably low number of Ross's geese, *Chen rossii*, set in motion a positive feedback loop, wherein grubbing for belowground plant parts caused vegetation cover decline and soil exposure, which led to the development of hypersaline topsoil, in turn killing off extant vegetation (Srivastava and Jefferies 1996), and reducing plant recovery potential (Handa et al. 2002). This resulted in—for avian herbivory—exceptionally large-scale denudation of, notably, saltmarsh habitat, and to a lesser extent also freshwater habitat, in and around snow goose colonies, all along the 2000 km-long Hudson Bay coastline (Jano et al. 1998; Jefferies et al. 2006). Because recovery is slow (freshwater marsh) or absent (saltmarsh; Peterson et al. 2013), lack of vegetation causes geese to move away and establish colonies elsewhere, resulting in further goose impacts across the region.

Similarly long-lasting, and large-scale, disruptions of the vegetation can now be observed across the Canadian Arctic. For example, between 1988 and 2011, well north of the Hudson Bay in Nunavut, a five-fold increase in area of exposed peat habitat, from 269 to 1373 km² in a 36,370 km² large study area, and a 48% loss of wet sedge meadow, were observed (Conkin and Alisauskas 2017). Although goose impacts in large parts of the Canadian Arctic remain limited, goose numbers are very high, colonies numerous, and local grazing impacts strong and replicated over large areas. Hence, region-wide ecosystem impacts are likely, including population declines of other bird species e.g., shorebirds and passerines (Flemming et al. 2016). Other Nearctic goose populations are less large, but otherwise following suit (e.g., Canada goose *Branta canadensis*, greater snow goose), and impact staging and breeding grounds elsewhere. Hunting pressure has been increased significantly in an attempt to curtail goose populations (e.g., Lefebvre et al. 2017), and reduce the pressure on arctic ecosystems as well as on agricultural land further south used by geese outside the breeding season, and which fuel the population expansions. Hunting has stabilised the population of greater snow geese (to around one million birds—Lefebvre et al. 2017), but the, more than an order of magnitude, more abundant population of lesser snow geese continues to grow despite huge hunting efforts (Alisauskas et al. 2011).

Whilst Palearctic goose populations expanded almost as spectacularly, impacts on their Arctic breeding grounds are far less pronounced. Pink-footed goose impacts,

which like snow geese are sufficiently powerful to dig for belowground plant parts (i.e., grubbing) early on in the breeding season (Anderson et al. 2016), do now occur throughout the productive parts of Svalbard, but with the initial disruption of the vegetation overlying organic soils recovering swiftly (Speed et al. 2010). Colony-breeding geese that do not have the physical ability to grub extensively, such as the barnacle goose, can locally also be influential—suppressing e.g., vascular plant and moss biomass and the carbon sequestration ability of tundra—but again recovery, when grazing pressure reduces, is rapid (Sjögersten et al. 2008, 2011), and hence is best not labelled “habitat degradation” (Van der Wal 2006). A fundamental difference with the coastal zone of NE Canada, subject to isostatic uplift (Jefferies et al. 2006), is the absence of saline subsoil; when exposed through grubbing, soils in the Hudson Bay turn hypersaline which kills the vegetation, and puts vegetation succession on long-term hold. Thus, waterfowl impacts on terrestrial ecosystems may be strong and long-lasting, but particularly so when amplified by specific abiotic conditions.

Extensive use of agricultural land—often superior in foraging quality to semi-natural habitats (e.g., Fox and Madsen 2017; Dokter et al. 2018)—by a growing number of grazing birds (Van Eerden et al. 2005), has attracted widespread disapproval among, notably, the farming community, leading to loci of conflict around specific species. Evidence for such grazing impacts is mixed (see Fox et al. 2017 for a review), but the conflicts remain real. Whilst overwintering species (of notably geese) were initially seen as most problematic by some, there is a shift towards a broader discontent about extremely rapidly growing populations of year-round bird species. Within Europe this concerns is expressed most prominently towards greylag geese (a species which has increased particularly rapidly—Fox and Madsen 2017), but also towards other expanding species originating, at least in part, from collections (e.g., Canada goose, Egyptian goose, *Alopochen aegyptiaca*, mute swan, barnacle goose, white-fronted goose, *Anser albifrons*). Increasingly, questions are being asked about how such summer herbivory may impact various ecosystem functions, including food stocks of migratory bird species arriving in autumn (e.g., Gyimesi et al. 2011). In many countries, resident waterfowl species have also penetrated into urban environments, and established sizeable populations. Their omnipresence, and diversity of impacts on society, ranging from fouling of lawns and pavements to aggressive encounters, air traffic accidents, and concerns about zoonotic diseases (Buij et al. 2017), has rendered several species subject to sometimes dramatic population control. The rapid expansion of, notably, geese, but also ducks, cranes, coots, wood pigeons and other species benefitting from almost unlimited feeding opportunities provided by farmland landscapes, and the resulting diversification of impacts, is leading to significant shifts in the dynamics of different interest groups’ views on the future of herbivorous birds (Cusack et al. 2018). This is an area of growing academic, political and conservation interest, and is likely to spill over into other areas of society, across large areas of the northern hemisphere (Milton 2000; Fox and Madsen 2017).

15.6 Marsupials

Ben Moore and William Foley

Amongst marsupials, browsers and grazers are found almost exclusively among the Australasian order Diprotodontia (Hume 1999), with significant herbivory not reported, and certainly unstudied, in South American marsupial lineages. This assemblage evolved in the absence of eutherian browsers and grazers, to occupy a diversity of ecological niches, throughout the Australian continent (Tyndale-Biscoe 2005). However, the diversity, size range and impact of marsupial browsers and grazers is much reduced from that prior to the Pleistocene extinction of megafaunal browsers including the short-faced kangaroos, *Simosthenurus* spp., the chenopod specialist, *Procoptodon goliah*, the “marsupial tapir”, *Palorchestes* spp., and the diprotodontines, *Euryzygoma* spp., *Diprotodon* spp. and *Zygomaturus* spp., (Johnson 2006; Prideaux et al. 2009). The only native Australian non-marsupial mammalian browsers and grazers are rodents, including the highly-specialised, vole-like grass-eating broad-toothed rat, *Mastacomys fuscus*, the swamp rat *Rattus lutreolus* and the arid-zone sticknest rats, *Leporillus* spp., (Breed and Ford 2007; Aplin and Ford 2014). Other omnivorous and primarily seed- and fruit-eating rodents (e.g., *Melomys cervinipes*), also include grass and leaves in their diets, to varying extents (Breed and Ford 2007). In consequence, marsupial browsers and grazers account for most Australian native vertebrate herbivory. The direct impacts of marsupial herbivory are rarely quantified, except where economic impacts occur, or are perceived, and where species are judged to be overabundant, and detrimentally affecting vegetation condition or biodiversity values (e.g., Barnes and Hill 1992; Coulson 2007; Di Stefano et al. 2007).

15.6.1 Marsupial Grazing

Grazing, as the main dietary habit amongst marsupials, is restricted to some species in the family Macropodidae (kangaroos and wallabies), and to all members of the family Vombatidae (wombats). Arman and Prideaux (2015) classified the diets of 37 extant macropods, and identified only 3 browsers (diet comprising >70% dicot foliage; these were two arboreal tree kangaroos and the small terrestrial quokka) and 9 grazers (>70% grass; large kangaroos and wallabies), while the greatest number (19) were mixed feeders. Previous classifications, with a greater emphasis on dental morphology, had identified many of these mixed feeders as browsers (e.g., Sanson 1989).

Because of their perceived economic impact, the impacts of large and abundant grazing marsupials have attracted the most attention from ecologists. Several species of large kangaroos, in particular red kangaroos (*Osphranter rufus*, formerly *Macropus rufus*—here we adopt the taxonomy of Jackson (2015)) together with

the euro/wallaroo, *Osphranter robustus*, and eastern grey, *Macropus giganteus*, and western grey, *M. fuliginosus*, kangaroos, often graze the same pastures as domestic livestock, and macropods including grey kangaroos can aggregate in crops, causing cereal production losses (Coulson 2007). Agile wallabies, *Notamacropus agilis*, and black-striped wallabies, *Notamacropus dorsalis*, are sometimes, locally, identified as pests of pasture and/or crops in northern Australia and Central Queensland, respectively (Baxter et al. 2001; Bedoya-Pérez et al. 2017).

There has been a long-standing debate about the extent to which these macropods and livestock, particularly sheep, compete for the same pasture resources. Demonstrating intraspecific competition is difficult, and the evidence, for competition between livestock and macropods, can only be considered insufficient to weak (e.g., dietary overlap with a lack of evidence that resources are limiting; Spear and Chown 2009, Prins 2016). In arid New South Wales, Dawson and Ellis (1996) found little dietary overlap occurred between sympatric euros and sheep, but a large manipulative experiment, in the same region, showed that the diets of red kangaroos and sheep overlapped considerably. This was true whether they grazed together or separately, but the degree of overlap varied with rainfall and available pasture biomass (Dawson and Ellis 1994; Edwards et al. 1995, 1996). Although sheep diets were affected, during dry times, by the presence of kangaroos (they consumed more chenopod shrubs), kangaroo diet was unaffected by the presence of sheep. It appears possible then that competition may occur when red kangaroos deprive sympatric sheep of pasture when pasture biomass is low, but moderate or strong support for either competition or facilitation between macropods and livestock, such as evidence of detrimental effects on individuals or populations of putatively competing species, is lacking (Edwards et al. 1995; Dawson 2012).

Australian rangelands are characterized by non-equilibrium dynamics, and at times both kangaroos and sheep can reduce pasture to an ungrazeable level (Short 1985), at which times food must become, at least transiently, limiting. Whilst primary producers can re- or destock, to rapidly alter grazing pressure as circumstances demand, the numerical response of kangaroo species, although high (Bayliss and Choquenot 2002), is sometimes insufficient to take advantage of the transient availability of good pasture. Red kangaroos, and perhaps, euros are exceptions in that they can travel long distances to take advantage of local rainfall events (Croft 1991; Clancy and Croft 1992).

Only weak evidence can be found for competition or facilitation between macropods and cattle. Consistent with competition, black-striped wallabies, *Notamacropus dorsalis*, show very strong dietary overlap with cattle in Central Queensland and consume economically very significant quantities of pasture (Baxter et al. 2001). In the Simpson Desert, removal of cattle resulted in a progressive increase in kangaroo numbers over a period of approximately 2 years compared to areas where cattle remained (Frank et al. 2016), but over the short duration of that study, kangaroo feed intake (estimated from dung deposition) remained a tiny fraction of that of cattle. More consistent with facilitation, time-series data, from across a large area of the South Australian pastoral zone, revealed that the presence of sheep and cattle had a positive effect on the population growth rate of red

kangaroos, although this result was interpreted by Jonzen et al. (2005) as indicating that livestock are a surrogate for resource availability beyond rainfall. At a smaller scale, Payne and Jarman (1999) observed immediate disturbance impacts of cattle on grazing kangaroos in eastern Australia and found these to be minimal, with kangaroo groups distributed more closely to cattle groups than expected by chance.

A second aspect of the debate about the impact of kangaroo grazing on domestic livestock focusses on the amount of food consumed by kangaroos relative to sheep. The safe stocking rate of rangelands for sheep is usually expressed in terms of “dry sheep equivalents” (DSE) which is the amount of food required to support a “typical” 2-year-old ~ 45 kg non-lactating Merino sheep (Turner and Alcock 2000). This unit is then used to compare different livestock management options. Dawson and Munn (2007) note that kangaroos are regarded, by some, as eating twice as much food as sheep (i.e., 2 DSE) but values of around 0.7 are typically assumed by Departments of Agriculture, because the basal metabolic rate of marsupials is generally about 70% of that of eutherian mammals (Munn and Dawson 2003). Dawson and Munn (2007) bring together data from many sources, including from heart-rate telemetry (Munn et al. 2009), and observations of bite rates (McLeod 1996) to estimate feeding rates of free-living kangaroos. They conclude that, on rangelands, kangaroos can be considered to be equivalent to 0.4 DSE in the event that competition is occurring.

Although much research has been directed towards the implications for domestic stock of grazing by kangaroos, attention is turning to the effects of grazing on ecosystems and biodiversity, particularly by high-density kangaroo populations. Grazing marsupials can engineer environments by maintaining lawns—bare-nosed wombats, *Vombatus ursinus*, can exclude woody plant establishment, and maintain lawns, in Tasmanian wetlands (Roberts et al. 2011), and both bare-nosed and hairy-nosed wombats, *Lasiorhinus latifrons*, can maintain lawns, in well-drained areas, elsewhere, by closely and repeatedly cropping their preferred tough native perennial grasses (Hume 1999; Tyndale-Biscoe 2005; Kirkpatrick 2016). Observations have been reported of up to 80 wombats grazing by day in some Tasmanian locations (Temby 1998). Red kangaroos can also maintain grazing lawns in Central Australia (and depend upon them during drought), but initial establishment of these lawns is facilitated by removal of senescent biomass by cattle (Newsome 1997).

Experimental studies have shown that high densities of kangaroos, at multiple locations in south-eastern Australia, have significant negative effects on ground layer plants (Sluiter et al. 1997; McIntyre et al. 2010, 2015), tree seedlings and saplings (Noble 2001; Meers and Adams 2003; Allcock and Hik 2004; Stapleton et al. 2017), beetles (Barton et al. 2011), grassland-dependent reptiles (earless dragons, *Tympanocryptis pinguicolla*, Howland et al. 2014, and striped legless lizards, *Delma impar*, Howland et al. 2016a), and reintroduced eastern barred bandicoots, *Perameles gunnii*, (Winnard and Coulson 2008). Browsing damage by kangaroos can be particularly significant during droughts, when grass biomass is depleted (Coulson and Norbury 1988). For several other groups, including web-spinning spiders (Foster et al. 2015) and birds (Howland et al. 2016b), the results were more complex with some species of birds being affected and others not.

In semi-arid, low-productivity Australian rangelands and woodlands, where kangaroos exist at more moderate densities, the intensity of their grazing is substantially less than that of livestock or rabbits, *Oryctolagus cuniculus*, (Vandendorj et al. 2017). Structural equation and multiple linear regression models that have been designed to identify the relative impacts of different types of herbivory and abiotic factors, suggest that the impacts of kangaroos on plant species composition (Travers et al. 2018), plant species diversity (Eldridge et al. 2018), shrub and tree short-term recruitment and long-term regeneration (Tiver and Andrew 1997), soil health (Eldridge et al. 2017) and regulating and provisioning ecosystem services (Vandendorj et al. 2017), are correspondingly benign, again in contrast to past and present impacts of exotic herbivores, particularly sheep. Indeed, under low productivity, kangaroo grazing can increase native plant species richness (Eldridge et al. 2018). In contrast, Rees et al. (2017) experimentally excluded kangaroos from plots in the Strzelecki Desert, demonstrating that in the absence of dingoes (*Canis dingo*), which otherwise suppress their numbers, kangaroos can suppress pasture biomass and grass seed production. This in turn likely contributes to the decline of small graminivorous birds.

Solutions to the impacts of high kangaroo densities are varied and can involve restoring coarse woody debris into habitats to protect saplings and create microhabitats for ground flora (Stapleton et al. 2017), direct reduction of kangaroo numbers through shooting (from densities of $\sim 2\text{--}4\text{ ha}^{-1}$ to as low as 0.4 ha^{-1}), and the possible re-introduction of apex predators such as the dingo (Letnic et al. 2009). Long-term studies indicate that grassland recovery, from heavy grazing pressure by kangaroos, can be a slow process, particularly if the grazing pressure from kangaroos is replaced by that of other herbivores, such as rabbits. Although direct reduction of kangaroo numbers is a simple long-term strategy, in some places there can be significant community and professional opposition to the process, and accompanying actions (Ben-Ami et al. 2014; McKinnon et al. 2018). Nonetheless, the four large kangaroo species are the focus of Kangaroo Management Plans, and permits for culling are assessed each year (Department of Parks and Wildlife, Western Australia 2013; Department of Environment, Water and Natural Resources, South Australia 2017; Department of Environment, Land, Water and Planning, Victoria 2017; Department of Environment and Heritage Protection, Queensland 2018). Southern hairy-nosed wombats and bare-nosed wombats are also occasionally culled under license, in response to perceived impacts on cereal crops and pasture (Marks 1998), although the impact of their digging and damage to fences is generally more problematic (Triggs 2009).

The potential also exists for competition between marsupial browsers and grazers and non-livestock herbivores species, most particularly rabbits. Strong, to very strong, experimental evidence has been presented to show that competition from rabbits negatively affects bare-nosed wombats (Cooke 1998) and red kangaroos (Cooke and Mutze 2018). Grazing by rabbits favours (often exotic) annual grasses and forbs over native perennial grasses, and these altered grasslands are less able to support the more protracted reproduction of marsupials (Tyndale-Biscoe 2005).

Both in Australia, and in its introduced range in New Zealand, the browsing common brushtail possum, *Trichosurus vulpecula*, sometimes feeds on pasture, particularly on clover, which can account for up to 30% of its diet (Harvie 1973). Possums have sometimes been considered to compete for pasture with livestock, with estimates of grazing equivalence as high as 0.072 stock units (SU; the New Zealand SU is for a 55 kg lactating ewe, so exceeds the Australian DSE) but a more convincing estimate is 0.01 SU (Cowan 2007). More strikingly, in Tasmania, the combined effects of possum and wallaby grazing have been suggested to reduce dry matter yields by up to 94% and 48% for improved and native pasture, respectively (Statham and Rayner 1995).

15.6.2 Marsupial Browsing

Marsupial browsing impacts can be attributed to browsing and mixed-feeding macropods, and a number of arboreal folivores. The arboreal folivores include several widespread and locally abundant species that specialize, to varying extents, on the foliage of eucalypts, and of these koalas, *Phascolarctos cinereus*, and common ringtail, *Pseudochirus peregrinus*, and common brushtail possums have all been linked to defoliation and mortality of trees, when they occur in high densities, although the impact of common brushtail possums has been most thoroughly investigated in its introduced range in New Zealand (Cowan and Waddington 1990; Pekelharing et al. 1998; Duncan et al. 2011).

In the absence of predation, or significant impacts of disease, koala populations can exhibit rapid population growth, resulting in population densities as high as 20 ha⁻¹, reported from Cape Otway, Victoria (Whisson et al. 2016). At high koala population densities, browsing is unsustainable, and results in widespread tree and koala mortality (Fig. 15.4) (either directly from starvation or from euthanasia of malnourished captured koalas by management agencies; Martin 1985a, b, Department of Environment, Land, Water and Planning, Victoria 2016) and loss of koala habitat, as well as posing a threat to certain vegetation classes and their associated biodiversity (Department of Sustainability and Environment, Victoria 2004). Localised events, like these, have been recorded repeatedly since the early twentieth century and occur most commonly in isolated patches of habitat on islands or surrounded by cleared land (Kershaw 1934; Menkhorst 2008). Koala overabundance is usually associated with *Eucalyptus viminalis* across a variety of soil types in coastal regions of Victoria and South Australia, although it can also develop in *E. ovata* and other species (Martin 1985a), and has been reported in association with *E. tereticornis* from northern coastal NSW (Frith 1978).

The population dynamics of koalas, in *E. viminalis* forest, have been well studied, and modelled (Todd et al. 2008; Whisson et al. 2016). Ramsey et al. (2016) estimated that the koala carrying capacity of the manna gum forest at Cape Otway is 5.3–8.3.ha⁻¹, but cautioned that this estimate has low precision, and may be too high to allow recovery of previously overbrowsed trees; an appropriate management



Fig. 15.4 Dense populations of arboreal browsing marsupials can cause severe overbrowsing of the forest canopy. In this forest at Cape Otway, Victoria, koalas have overbrowsed and killed all mature manna gum, *Eucalyptus viminalis*, trees, while the less preferred messmate stringybarks, *E. obliqua*, have survived. Photo Credit: Ben Moore

target for a “safe” population density is probably lower than this estimate. Most koalas show strong fidelity to their small home ranges (0.4–1.2 ha at Cape Otway; Whisson et al. 2016), even in the face of declining food resources, and despite adequate habitat connectivity making dispersal possible. A model of koala-manna gum dynamics, at Mt. Eccles in western Victoria, predicted the koala population increasing to peak abundance in 10–18 years before crashing—with the impact on tree mortality dependent upon the eventual maximum rate of decline of the koala population (Todd et al. 2008). Eucalypts have a remarkable capacity to replace foliage after defoliation or fire, but energy (starch) reserves can be depleted if repeated defoliation occurs over an extended period (Bamber and Humphreys 1965). A management strategy, suggested by Todd et al. (2008) on the basis of their modelling, requires the sterilization of a variable number of female koalas each year in order to maintain a fixed number of non-sterilised females. Chemical (and formerly, surgical) sterilization (Hynes et al. 2010) is a widely-implemented koala management strategy in South Australia and Victoria, as is translocation of koalas from overabundant populations.

Increasingly, koalas are now reaching high densities, in commercial plantations of *E. globulus* established in the 1990s in Victoria and South Australia (Natural Resources Kangaroo Island 2017, Department of Environment, Land, Water and Planning, Victoria 2018; Department of Environment, Water, and Natural Resources, Government of South Australia 2017). Although significant impacts on

plantation productivity have not been claimed (nor measured), costs to the plantation industry are considerable, because harvesting operations must be modified, and significant reputational cost is incurred by forestry companies when koalas are killed or injured (e.g., ABC News 2013; HVP Plantations 2018). Marsupial browsing of eucalypt seedlings in Tasmanian hardwood plantations, is more obviously detrimental to productivity, because it reduces seedling growth and survival and affects tree form (Bulinski and McArthur 1999; Scott et al. 2002). Consequently, Tasmania has implemented intensive browser control measures and encouraged research into the problem (e.g., Miller et al. 2009; Close et al. 2010; Miller et al. 2011). While brushtail possums, pademelons and wallabies have all been implicated, Bulinski and McArthur (2003) suggested that the relative contribution of brushtail possums had previously been underestimated.

The second specialist folivore of eucalypts (in addition to the koala) is the greater glider, *Petauroides volans*, which does not appear to reach population densities that measurably affect tree canopy biomass. However, the two generalist browser species, that can feed to significant extents on eucalypt foliage, i.e., the common brushtail and ringtail possums, can both occur in very high densities, and can cause local canopy loss and eucalypt mortality (Loyn and Middleton 1980; Low 2002; Yugovic 2015).

Dramatic impacts of common brushtail possums, on native vegetation, have been reported when they have been introduced to islands, such as the Keppel Islands in Australia, and most famously, to New Zealand (Low 2002). Possums selectively browse on, and cause crown dieback of, numerous native forest trees and mistletoes in New Zealand (Sweetapple 2008; Sweetapple et al. 2016), and enormous efforts are expended to reduce and control possum populations. Holland et al. (2013) have produced a model to describe the impact of browsing by common brushtail possums on woody vegetation, and have parametrized, and run, this model for several NZ tree species (Holland et al. 2016). These models focus on tree mortality as an endpoint, and key input parameters are plant foliage cover, and an index of browse damage. These models are constructed such that the relationship of possum density to tree mortality is strongly non-linear, and high possum densities are required before browsing impacts become apparent. A strength of these models is the recognition, by the modellers, that browsing is selective at the level of browse species and individual plant (Windley et al. 2016). While many other modellers (e.g., Feng et al. 2009) average herbivore offtake evenly across plants in the landscape, the models of Holland and coworkers incorporate the recognition that herbivory is often concentrated on individual, preferred trees. Selective browsing, including that driven by strong differences in secondary chemistry among conspecific individual plants (e.g., Moore et al. 2010), explains why browsing impacts can become apparent even when overall herbivore densities appear to be too low to have an impact on foliar production at the ecosystem level. These models have not yet been applied to Australian eucalypts, although these trees might differ from the New Zealand examples used by Holland et al. (2016), in terms of leaf lifespan, carbohydrate storage and bud reserves to facilitate regrowth, and may show greater-between tree variability in herbivore preferences attributable to plant secondary metabolites.

As with grazing, browsing by marsupials can affect biodiversity, especially by limiting regeneration of tree species after disturbance (Allcock and Hik 2004). Overabundance of the mixed-feeding swamp wallaby, *Wallabia bicolor*, at Booderee National Park, in coastal NSW, suppresses regeneration of *Eucalyptus pilularis* seedlings, as well as other native and weedy trees, vines and shrubs, favouring the growth of bracken, *Pteridium esculentum*, (Dexter et al. 2013). Stutz et al. (2016) demonstrated the remarkable ability of these wallabies to locate and target small seedlings by olfaction, even when they are obscured by thick understorey. Exclosures were also used at Wilsons Promontory, Victoria, to demonstrate that secondary succession (from shrubland to forest) could only proceed in the absence of swamp wallabies, which were capable of pulling down and browsing saplings as tall as 2 m (Ashton and Chappill 1989). In different Victorian forests, swamp wallaby effects on forest regeneration, after harvesting, can range from minimal (Di Stefano et al. 2007) to substantial (Di Stefano 2005). Browsing can also, sometimes, threaten individual plant species such as the Tasmanian trees *Eucalyptus gunnii* (Calder and Kirkpatrick 2008) and the threatened *Eucalyptus morrisbyi*, in which one of two remaining populations is less able to resist brushtail possum herbivory, and suffers lower flowering as a consequence (Mann et al. 2012).

Both the burrowing, *Bettongia lesueurii*, and the rufous, *Aepyprymnus rufescens*, bettongs differ from the other, principally mycophagous, rat-kangaroos in consuming significant amounts of plant material. Although this is generally thought to comprise mostly roots and tubers (Claridge et al. 2007), foliage and branches can also be consumed, particularly in high-density populations (Bice and Moseby 2008; Linley et al. 2017). Woylies, *Bettongia penicillata ogilbyi*, too, include substantially higher amounts of plant food in their diet in a high-density, food-limited, fenced population than they do otherwise (Zosky et al. 2018). Anecdotally, bettong browsing has been suggested to have limited post-fire recruitment of eucalypt seedlings (Noble et al. 2007), and the decline of rufous bettongs was linked, again anecdotally, to increased recruitment of woody vegetation in western New South Wales (Rolls 1981). Noble et al. (2007) modelled the impact of browsing by burrowing bettongs, fire and rainfall on shrub population dynamics and suggested a potential for fire and browsing, either individually or in combination, to maintain low shrub densities.

As with grazing marsupials, the impacts of browsing marsupials may only become apparent in the absence of mechanisms that would otherwise suppress populations, or alter their foraging behavior (Pickett et al. 2005). This could include the cessation of hunting by humans, and a lack of predation by native owls (e.g., Kavanagh 1988), raptors and dingoes, due to human persecution, local extinction or exclusion from fenced reserves. The isolation of habitat patches, due to land clearing and the introduction of marsupial herbivores to islands, can also make dispersal impossible, thereby increasing population growth rates. For example, burrowing bettongs previously declined to extinction on mainland Australia, but now thrive in predator-exclusion reserves such as Arid Recovery in South Australia, where their densities are sufficient to reduce perennial plant species richness and reduce vegetation condition (Linley et al. 2017). These effects were not seen at lower

bettong densities in the same habitat (Munro et al. 2009). Similarly, browsing by quokkas, *Settonix brachyurus*, acts, together with fire, to prevent tree seedling recruitment on Rottnest Island, Western Australia (Main 1992).

15.6.3 Conclusion

Australian mammalian herbivore communities have changed dramatically since the arrival of humans, which was followed by the loss of browsing and grazing mega-fauna. Not only the causes of these extinctions, but also their consequences continue to be debated, as researchers struggle to attribute evidence of changed vegetation to herbivory, fire and climate (Johnson 2006). Given the former diversity of large mammalian herbivores, one can imagine an impact on par with that of African herbivores today. A second wave of ecosystem change commenced with the invasion of Australia by Europeans 230 years ago. Since then, woody vegetation clearance, changes to fire regimes, provisioning of water, pasture improvement, and the introduction of exotic weedy and pasture species, have altered the environment in which marsupials forage. Australia's apex predator, the dingo, has been rendered functionally extinct in large parts of the country, while exotic mesopredators such as the fox have had devastating impacts on many smaller mammalian herbivores. Grazing herbivores now coexist alongside, and possibly compete, with exotic sheep and cattle, rabbits, camels, goats and pigs, which themselves alter the foraging environment encountered by native marsupial herbivores (e.g., Cooke 1998; Tyndale-Biscoe 2005). As they have disappeared from across the landscape, or as the ecosystems around them have been altered, the prospect of understanding the former ecological role of many marsupial herbivores has slipped from our grasp, but much also remains to be learnt about their contemporary impacts.

15.7 Lagomorphs

Lucy Lush

Lagomorphs are small- to medium-sized mammals that inhabit a wide variety of habitats worldwide, both as native or introduced species (Hutchings and Harris 1996; Trout 2003). The lagomorph Order includes hares, *Lepus* spp., rabbits, *Leporidae* spp., and pikas, *Ochotonidae* spp., many of which are classed as endangered in their native ranges, with introduced species often becoming pests (Cowan and Hartley 2008; Jennings 2008). Despite their small size, lagomorphs can dramatically shape vegetation structure and composition, both positively and negatively (Boag et al. 1990; Crawley 1990; Van der Wal et al. 2000a, b; Stahl et al. 2006). The way land is managed can equally affect the distribution and behaviour of lagomorphs (Petrovan et al. 2013; Lush et al. 2014). Understanding the determinants of

lagomorph distribution and behaviour, and interactions between these species and the ecosystems they inhabit (Sinclair et al. 2000), could provide management solutions for both conservation and biosecurity.

15.7.1 Feeding Ecology of Lagomorphs

Lagomorphs are selective feeders and can be both grazers and browsers, depending on the habitat, season and food availability (Chapuis 1990; Schai-Braun et al. 2015). In general, lagomorphs graze on grasses and herbs but may browse on saplings and woody plants, particularly when forage resources are limited during winter (Homolka 1982; Rao et al. 2003). Some species of hares, such as the Mountain hare, *Lepus timidus*, are specialist browsers, preferentially feeding on deciduous tree species (Hjältén et al. 2004).

Lagomorphs are hind gut fermenters and, unusually, they perform coprophagy (re-ingesting the soft faeces initially produced after a feeding bout) that enables them to more effectively digest lower quality forage (in comparison to other mammalian herbivore species their size) (Kuijper et al. 2004). This allows their diet to be incredibly varied and provides the flexibility to adapt to changes in plant availability, management of agricultural land or competition from other herbivores.

Rabbits and pikas are central placed foragers, which results in grazing gradients, with reduced grazing intensity and increased dietary selectivity in grasslands further away from their burrows or talus (Huntly 1987; McIntire and Hik 2005; Bakker et al. 2005). This can lead to higher standing biomass, vegetation height and decreased plant nutrient concentration at greater distances from burrows (Bakker et al. 2005). Unlike rabbits, pikas also carry out haying (caching plants) during periods of high vegetation biomass, enabling them to survive through periods when vegetation is dormant (Huntly et al. 1986). In contrast, hares often select fields with taller vegetation that provides cover from predation, and less intensively managed agricultural land, with higher levels of fat in plant material, whereas rabbits select for more intensively livestock grazed pastures with nitrogen rich shorter grass (Bakker et al. 2005; Lush et al. 2014, 2017).

15.7.2 Impacts of Lagomorph Grazing and Browsing

The flexible feeding ecology of lagomorphs can affect, both positively and negatively, the localised impact of their grazing behaviour on the landscape. For example, rabbits and pikas usually graze close to their burrows, which creates high intensity grazing areas (Huntly et al. 1986; Cowan et al. 1989). Hares can also affect vegetation structure through selectively browsing on plant species (Rose and Platt 1992), reducing woody biomass (Pease et al. 1979) and removing seedlings (Wong and Hickling 1999). This can benefit other species, for example, hare browsing

restricted the growth of shrubs such as, *Artemisia maritima* and *Atriplex portulacoides*, on salt-marshes that created preferential foraging habitat for Brent geese (Van der Wal et al. 2000b). High population densities of lagomorphs can, therefore, lead to fundamental alterations to grassland structure and composition (Boag et al. 1990; Crawley 1990), and can cause damage to native grasses and forbs, resulting in reduced species richness, reduction in the area of grassland swards and increased weeds (Mutze et al. 2016). Studies, using exclusion experiments, revealed that preferential grazing of certain plants by lagomorphs reduced plant diversity and vegetation growth (Gibbens et al. 1993; McIntire and Hik 2005). However, these effects can be confounded by grazing by other types of herbivores, weather conditions and long-term effects of grazing pressure.

European rabbits, *Oryctolagus cuniculus*, have become a significant pest species in many countries (Cowan 1987). In the UK, damage to crops have been estimated at £115 million annually (Smith et al. 2007), and, in Australia are attributed to the loss of A\$206 million in agriculture (Gong et al. 2009). However, rabbits can provide commercial revenue for example, A\$36 million in Australia from the sale of products as a result of shooting (Gong et al. 2009).

Rabbit grazing can also benefit the environment, providing an important mechanism for maintaining certain habitats such as, calcareous grasslands, heathland and sand dune grasslands (Lees and Bell 2008; Trout 2003). When rabbits were removed from these habitats, plant biodiversity reduced and indirectly affected numbers of important invertebrate species (Barham and Stewart 2005). Similarly, the burrowing and grazing activity of pikas, *Ochotona pallasi*, has improved soil nutrients in arid habitats, and subsequently increased grass productivity, creating higher species diversity and vegetation abundance (Wesche et al. 2007; Yu et al. 2017). Although, in contrast, other studies found they had little impact on grassland plant species richness, and pikas were negatively affected by high intensity livestock grazing (Komonen et al. 2003).

Being prey species, lagomorphs can, to some extent, be naturally controlled by predators, such as the red fox, *Vulpes vulpes*, and lynx, *Lynx lynx*. There has been a 10 year cyclic relationship between snowshoe hare populations, *Lepus americanus*, and lynx, in North America, through a combination of predation and forage quantity and quality (Krebs et al. 2001). Similarly, rabbits, in their native ranges, are declining due to changes in land use, habitat loss and introduced viruses, resulting in declines in lynx populations (Virgós et al. 2003; Lees and Bell 2008). The changes in population density of lagomorphs can, in turn, affect grazing pressure, plant growth and composition.

15.7.3 Effect of Management on Lagomorphs

Agricultural intensification, and changes in management practices, have altered the habitat and food availability for lagomorphs. The winter planting of agricultural crops has provided an important food source for hares and rabbits, when other

natural forage resources are limited; inadvertently resulting in an increase in rabbit populations (Tapper and Barnes 1986). Removal of hedgerows, woodlands and the planting of larger, monocultural fields, reduced habitat diversity and structure, which has negatively impacted some lagomorphs, such as the brown hare, *Lepus europaeus*, that require a diverse variety of plants and habitat structure (Tapper and Barnes 1986). Increased livestock grazing reduces the available forage and cover for lagomorphs, and has been shown to have a major impact on lagomorphs' foraging distribution (jackrabbits, cottontails and brown hares), with higher numbers found on areas with moderate livestock grazing, as opposed to those areas that were heavily or lightly grazed (Milchunas et al. 1998; Karmiris and Nastis 2007). This could also create potential competition for resources between livestock and lagomorphs (Hulbert and Andersen 2001). Livestock grazing regimes, the application of fertiliser and planting different grass or crop species affects plant nutritional quality and, consequently, lagomorph diet (Bakker et al. 1983; Pavlů et al. 2006; Lush et al. 2017). In particular, the amount of nitrogen, crude fat and fibre available in plants have differing effects on lagomorph foraging distribution and body condition (Hackländer et al. 2002; Bakker et al. 2005; Lush et al. 2014).

15.7.4 *Managing Lagomorph Grazing and Browsing*

Biocontrol agents, such as, myxomatosis and rabbit haemorrhagic disease virus, were introduced in several countries to reduce the extremely high rabbit populations. Following the introduction of these agents, rabbit numbers in the UK reduced by 99.9% (Boag 1987), resulting in dramatic changes to the landscape, with increased grassland growth and regeneration of woodlands. The reduction in rabbit populations in the UK reduced plant diversity resulting in the extinction of some invertebrates, such as, the large blue butterfly, *Maculinea arion*, (Sumption and Flowerdew 1985). It also resulted in the decline of many predators that fed largely on rabbits such as, the stoat, *Mustela ermineu*, and buzzard, *Buteo buteo*, (Sumption and Flowerdew 1985); with knock on positive and negative effects on the environment and economy. Eradication, and control, of introduced rabbit populations, particularly on islands, has resulted in increased plant species richness and cover, although exotic plants often populate areas faster than native plants, highlighting the benefits of rabbit grazing in some situations (Schweizer et al. 2016). In Australia, the reduction of rabbits benefitted Australian agriculture by A\$70 billion dollars (Cooke et al. 2013). Although, recently, increasing resistance to the virus, and different strains, have reduced the effectiveness of this control measure (Ross and Sanders 1984).

Less dramatic methods to control lagomorph populations and foraging behaviour can be mediated through changes in the structure and composition of available habitats (Boag 1987). Reduction of vegetation cover, removal of field boundaries and the use of set asides (removing areas of land from crop production creating strips of grassland at field edges), have reduced some crop losses from lagomorph grazing;

however, at high lagomorph densities these become ineffective (Trout 2003). Studies found that planting of older, larger tree saplings reduced lagomorph browsing in plantations (McArthur and Appleton 2004); similarly, reducing tree planting density, and planting seedlings in tall vegetation to reduce their visibility, lowered browsing pressure by hares (Rao et al. 2003). Less intensive farming practices, such as reducing livestock grazing and other inputs to pastures e.g., fertilisers that alter the nutritional value of vegetation, could benefit some lagomorph species (Lush et al. 2014). However, each lagomorph species has differing nutritional requirements and therefore, changes could be positive or negative. Further research, and regular monitoring, is required to assess the impact of different management practices on lagomorph species and measure the effectiveness of management interventions at a landscape scale.

15.8 Rodents

Renan Maestri

Rodents outnumber all other orders of mammals, in term of number of species (Wilson and Reeder 2005); approximately 42% of mammals are rodents, which corresponds to around 2400 species. Rodent radiations have occurred repeatedly across the globe, and they occupy all continents with the exception of Antarctica (Lacher et al. 2016), showing a parallelism in morphological and ecological features in each radiation (Wood 1947; Aplin and Ford 2014). The success of rodents in colonizing different environments is directly related to rodent's ability to exploit diverse food items, such as grasses, roots, leaves, fruits, seeds and insects. However, most rodents are herbivorous, or include some plant material in their diet, and have many adaptations for herbivory (Samuels 2009). This is apparent from the smallest rodents such as the pygmy jerboa, *Salpingotulus michaelis* (~4 g), that feed on desert-adapted leaves, to the largest living rodent, *Hydrochoerus hydrochaeris* (~60 kg), that feed on grasses, and even the largest extinct rodent, *Josephoartigasia monesi* (~1000 kg), is thought to have fed on soft vegetation and fruits (Rinderknecht and Blanco 2008).

A classification of rodents into browsing vs. grazing categories is uncommon compared to more traditional categories that divide rodents into chewing vs. gnawing for feeding habits, and into folivory (leaf eaters) vs. grammivory (grass eaters), among others, for food preferences. A comparative assessment of adaptations for herbivory, considering these categories, reveals many morphological and physiological differences among living rodents, which are reflected in their impact on the ecosystems through feeding activities, reviewed below.

The herbivorous habit of rodents is related to their characteristic skull shape, with enlarged and ever-growing incisors that are adapted for biting (also gnawing) (Lacher et al. 2016). The check teeth, which are found behind the incisors and the diastema, are effective at chewing and grinding of plant material. Gnawing with the

incisors and grinding with the check teeth are the main activities performed by rodents whilst feeding. Both functions take place in alternation: when the incisors are engaging, the jaw is positioned forward in a position that means that the check teeth do not meet each other; when the check teeth are positioned for grinding and chewing, the incisors are not positioned to allow gnawing (Vaughan et al. 2015). This difference in position relates to a trade-off between specialization for gnawing or chewing, and rodents can be roughly classified depending on their jaw musculature and skull adaptations for increased gnawing over chewing or vice versa (Cox et al. 2012).

Morphological adaptations for feeding, mainly related to the position and form of masseter muscles, can be used to segregate rodents in three non-monophyletic groups: sciuriform, hystricomorph and myomorph (Simpson 1945). In the sciuriform rodents the masseter lateralis and temporalis muscles are relatively large and the masseter lateralis extends onto the rostrum (Korth 1994). This leads to changes in feeding processes that, together, increase the gnawing abilities of these rodents. Greater gnawing abilities are associated with feeding on large seeds, nuts and roots. Examples of sciuriform rodents are squirrels, beavers and pocket gophers. In the hystricomorph rodents it is the masseter medialis that is greatly developed and extended, passing through an enlarged infraorbital foramen before attaching to the rostrum (Wood 1965; Korth 1994). Rodents with this adaptation have an increased ability to perform varied movements with the jaw, resulting in an improved capacity for chewing and grinding at the same time (Cox et al. 2012). These adaptations allow increased processing efficiency when feeding on plant material, and most strictly grazing rodents have this morphotype. Examples of hystricomorph rodents are jerboas plus some Old-World rodents, the South American porcupines and many other caviomorph species; the largest rodent in the world, the South American capybara, *Hydrochoerus hydrochaeris*, is a grazing rodent with these features (Herrera 2013). The myomorph rodents have a combination of features from both the sciuriform and the *hystricomorph* morphotypes, where the masseter lateralis extends onto the rostrum, as in sciuriforms, and the masseter medialis passes inside the infraorbital foramen, as in hystricomorphs (Korth 1994). This combination of features produces a phenotype capable of performing both gnawing and chewing functions that leads to effective feeding on seeds, fruits, grains and plant material in general (Cox et al. 2012; Maestri et al. 2016).

Dietary shifts also trigger corresponding changes in the shape of the jawbone (e.g., Hautier et al. 2012; Maestri et al. 2016). A narrow angular process of the mandible is usually associated with the hystricomorph rodents, while a more robust angular process characterizes sciuriformity. Even among hystricomorphs, those families feeding exclusively on grasses have a narrower and thinner angular process than those feeding on fruits and seeds (Hautier et al. 2011). Furthermore, a shorter, and curved, diastema, and a deeper ramus, characterize families that feed on fruits and seeds, as opposed to those that feed on grasses (Hautier et al. 2011). Other general differences in skull morphology occur according to whether a species feeds on grasses versus fruits and seeds (see Hautier et al. 2012), and still another set of

morphological characteristics are found among rodents that feed on meat (e.g., Woollard et al. 1978; Rowe et al. 2016).

Herbivory in rodents can also be augmented by adaptations of the teeth (e.g., Willians and Kay 2001; Ma et al. 2016). Hypsodonty, one of the hallmarks of herbivory for mammals in general (**Saarinen** Chap. 2), is also a feature of herbivorous rodents. High crowned cheek teeth can increase the capacity for processing plant material consumed during grazing, and these type of teeth are found, for instance, among caviomorphs and several species of small rats and mice. A few studies of South American sigmodontines rodents have shown that the proportion of high-crowned teeth is greatest in species found in cold and dry and semiarid climates, while few high-crowned species are present in wet and hot climates (see Madden 2015). In addition, high teeth crowns, and larger cheek teeth, are positively correlated with the more seasonal and open environments (Madden 2015; Maestri et al. 2017).

Another related adaptation is the development of ever-growing cheek teeth in some caviomorph rodents such as the caviids and chinchillids. Nevertheless, relating hypsodonty to diet in rodents is limited by the scarcity of work on dietary composition for rodents in general (Madden 2015; Arregoitia 2016). Analyses of stomach contents using, for example, metabarcoding (Lopes et al. 2015), have revealed a great overlap in plant families consumed by rodent species. Intestinal physiology studies can contribute by comparing the concentration of types of bacteria between rodents and grazing ungulates, revealing, for example, a similarity in intestinal physiology between the capybara and bovids (Borges et al. 1996, see Herrera 2013 for a distinction between foregut and hindgut fermenters). Enamel microwear investigations are also a useful tool that helped to classify grazing and browsing mammals (Townsend and Croft 2008), and are applicable to distinguish food preferences (e.g., omnivore, frugivore, granivore) among rodents (Caporale and Ungar 2016). Multiple approaches are urgently needed to analyse rodent diet composition, so as to move away from the broad description of rodents as “opportunistic” and “omnivorous”.

Given the diversity and wide geographical distribution of rodent species, and the propensity of its members to feed on many types of plant material, it is important to understand how the foraging behavior of rodents impacts ecosystems through grazing and browsing activities. A few studies have investigated the impacts of rodents on ecosystems through grazing (e.g., Howe et al. 2002; Bilodeau et al. 2014) and browsing (Ravolainen et al. 2014), yet most of the literature has focused on large mammals or rabbits (previous section **Katona and Coetsee** Chap. 12). Nevertheless, the impact of grazing rodents could be, at least, as great as that of rabbits at some regions, as in South America: Madden (2015) suggests that the invasion of South America by herbivorous caviomorph rodents (see also **Saarinen** Chap. 2) could have generated increased soil erosion resulting from their grazing activities. For example, there is evidence that the feeding behavior and burrowing activities of tuco-tucos (genus *Ctenomys*) reduces forage and leads to vegetation changes and habitat degradation (Jackson 1988). When these rodents cover large areas, they can alter the soil dynamics and the vegetation growth (Massoia 1970; Galiano et al. 2014). Similarly, the feeding behavior of vizcacha (genus *Lagostomus*), another caviomorph, can lead to reductions in vegetation cover and abundance and they even

compete with livestock for food; they are considered a pest in some areas of Argentina (Jackson 1988).

The effects of grazing and browsing of small rats and mice might also impact ecosystems, but may go unnoticed due to the difficulty of measuring their impacts. Limited direct evidence exists on the role of small cricetid rodents in damaging pastures and being pests of cultivated plants (Jackson 1988). Nevertheless, damage of human cultivated crops, such as rice and cereal grains, by small rodents, has been estimated to cause a billions of dollars per year of damage worldwide (Lacher et al. 2016). Using experimental plots in England, Hulme (1994, 1996) compared the impact of small rodents and invertebrates on seedlings predation and the growth of grasslands. He showed that rodents and molluscs had similar negative effects on herbaceous seedlings, consuming about 30% within a given plot. Nevertheless, rodents had their greatest effect on the growth of grassland plants, being responsible for a 50% reduction in mean plant biomass, greater than the impact of molluscs or arthropods. Hagenah et al. (2009) found a proportionally higher effect of murid rodents on plant biomass in a South African savanna, after excluding large herbivores from experimental plots; the exclusion of large herbivores had the effect of increasing small rodent abundance (Hagenah et al. 2009; Luza et al. 2018). Howe and Brown (1999) compared the effects of herbivory between small browsing rodents and birds in a tallgrass prairie, and found that the voles had negative effects on grass biomass and altered plant community structure, especially in low-density communities; while the effects of bird were more pronounced in high-density plantings. Browsing voles, such as *Microtus pennsylvanicus*, can even be considered a plague in prairie grasslands in North America, because they can cause drops in plant diversity (37% drop in Simpson's diversity index), greatly altering community composition (Howe et al. 2002).

Other studies have found contrasting results, showing that rodents have negligible top-down control on plant assemblages, which were mostly regulated by bottom-up processes, such as in native grasslands of North America (Báez et al. 2006). Similarly, grazing by lemmings had very weak effects on plant biomass at the Canadian arctic (Bilodeau et al. 2014). Therefore, while rodents have a pronounced effect on growth of grasses in some cases, the literature on the effects of browsing and grazing by rodents shows varying overall impacts on ecosystems. Furthermore work is needed, not just focusing specifically on rodents but also comparing the effects of rodents with those of large mammals, to reach a consensus about how great are the ecosystem impacts of grazing and browsing by rodents.

15.9 Primates

Ikki Matsuda and Marcus Clauss

Non-human primates (hereafter referred to as 'primates') cover various trophic niches, from nearly exclusive folivory to frugivory, gummivory, insectivory and omnivory; although the majority of species are folivorous, frugivorous, or both

(Campbell et al. 2011). One exceptional species, the gelada baboon, *Theropithecus gelada*, was thought to be graminivorous (a ‘grazer’); however, a recent study showed that geladas also consume a substantial amount of non-grass (non-monocot) foods, implying that they are not strict grazers as previously thought (Fashing et al. 2014). Folivorous primates that exhibit hindgut and foregut fermentation such as colobines (foregut fermenters: Asia and Africa), lemurs (hindgut fermenters: Africa) and gorillas (hindgut fermenters: Africa) are widely distributed in the Old World, and hindgut fermenting howlers are found in the New World (Mittermeier et al. 2013). Recent studies on the feeding ecology of some primates, technically classified as folivorous, have reported high levels of fruit and/or seed consumption in response to local habitat conditions (Campbell et al. 2011). Thus, classifying primates as strictly folivorous is not a simple matter.

15.9.1 Anatomical Adaptations to Diet

In parallel to the dichotomy of hindgut and foregut fermenters seen in mammals, primates generally have two contrasting digestive strategies: high intake with fast throughput for low digestive efficiency or low intake with slow throughput for high digestive efficiency (Clauss et al. 2008). Folivorous primates that exhibit foregut fermentation are mostly limited to the high digestive efficiency strategy (Clauss et al. 2008). Another key digestive strategy in folivorous primates entails fine-tuning of salivary protein composition. Howler monkeys, the most folivorous New World primates, show continuous expression of tannin-binding salivary proline-rich proteins; this allows them to consume a diet with variable tannin content (Espinosa Gómez et al. 2015). Such salivary tannin defences have been demonstrated in a few primate species, including omnivorous baboons and macaques (Espinosa-Gómez et al. 2018). On the other hand, as do a great variety of other grazing mammals, graminivorous geladas completely lack proline-rich proteins, and a capacity to bind tannins, demonstrating their narrower dietary niche compared to that of other baboon species (Mau et al. 2009). Given that colobines generally have large salivary glands, they may use a similar strategy to howlers (Kay et al. 1976; Matsuda et al. 2017b); however, this hypothesis awaits further testing.

The microbial community in the gastrointestinal tract is believed to play an important role in facilitating the consumption of hard-to-digest foods, such as leaves of trees and grasses. As a result of recent developments in sequencing technology, gut microbiota analysis, based on large amplicon libraries of 16S ribosomal RNA (rRNA) genes and mostly faecal DNA, has increasingly been conducted on folivorous primates (Ley et al. 2008). In folivorous primates, the distal gut microbiome varies even within a species according to diet and/or living conditions (Amato et al. 2013; Clayton et al. 2017); gut microbial diversity in captive primates is generally reduced compared with that in their wild counterparts. A recent study suggested that gastrointestinal distress in folivorous primates, such as infestation with or disease caused by parasites, may be associated with an imbalance between

the types of organism present in their natural microflora, especially that of the gut (Amato et al. 2016).

Nutritional studies have revealed that both hindgut and foregut fermenters generally prefer leaves rich in protein and lower in fibre (Ganzhorn et al. 2016). However, there are some folivorous primates that do not display a strong preference, indicating that a preference for protein depends on the overall protein availability in the environment; the preference for protein is only clearly demonstrated in environments with a low average protein content (Ganzhorn et al. 2016). Other factors that may affect dietary selection in folivorous primates are mechanical toughness and leaf digestibility. However, little information is available regarding primates' dietary choices, and studies evaluating a variety of nutritional and mechanical factors with diet digestibility are particularly lacking. One study providing new insights into *in vitro* digestibility, toughness and nutrients of leaves shows that the preferred leaves of foregut fermenting proboscis monkeys not only contain more protein and less fibre but are also less tough and more digestible than the alternatives (Matsuda et al. 2017b).

15.9.2 Behavioural Adaptations to Diet

The way a primate rests could be related to their digestive physiology. Among folivorous primates, this is most evident in colobines, that have a characteristic long resting period (over 70% of daylight hours) sitting with a vertical posture (Matsuda et al. 2017a). This might be because the position of the digestive chamber, and the need to frequently eructate digestive gases, force colobines to assume a posture that reduces pressure on the thorax and respiratory organs. In contrast to ruminants that are characterised by a sorting mechanism in their forestomach that operates based on the density of different-sized food particles (Lechner-Doll et al. 1991), with smaller particles generally having a higher density than larger ones (Clauss et al. 2009), experiments with captive colobines have shown no evidence for a forestomach sorting mechanism (Schwarm et al. 2009; Matsuda et al. 2015, 2019). Passage studies in general suggest that, as a group, primates do not pass solutes faster than particles, i.e., lack the physiological or mechanical ability to wash particulate digesta with fluids in the digestive tract that has evolved in all other mammalian herbivore clades (Müller et al. 2011). An interesting peculiarity is that a non-obligatory rumination-like behaviour has been demonstrated in one colobine species, the proboscis monkey (Matsuda et al. 2011; Matsuda et al. 2014).

As with most primates, folivorous primates live in groups varying in their sex-composition and -dispersal, e.g., one-male-multi-female or multi-female-multi-male groups with both-sex-dispersal or female-philopatric/male-dispersal. As leaves are generally abundant and evenly distributed in their habitats, socioecological models indicate that food competition within folivorous primate groups can be assumed to be weak/absent and that populations and groups are not constrained by the availability of food (Wrangham 1980; Janson and Goldsmith 1995; Sterck et al.

1997). Increasing day range with increasing group size has been used as a behavioural indicator of food competition within primate groups, and this hypothesis on weak/absent of food competition is supported by the fact that a flat relationship exists between group size and day range across various folivorous primates (e.g., Yeager and Kirkpatrick 1998). However, many folivorous primates, despite this assumed lack of feeding competition within their groups, often live in relatively small groups, though larger groups are expected to have lower costs of predation due to better detection of predators. This inconsistency is referred to as the ‘folivore paradox’ (Steenbeek and van Schaik 2001). Indeed, the results contradict the assumption of leaves as ubiquitous or non-patchy resources in some colobines, e.g., red colobus, *Procolobus rufomitatus*, (Snaith and Chapman 2005) and gray langurs, *Semnopithecus entellus*, (Sayers and Norconk 2008). Infanticide has been suggested as a mechanism that could regulate group sizes in groups with a high proportion of males, although this theory alone cannot explain the folivore paradox in all cases (reviewed by Snaith and Chapman 2007).

15.9.3 Conservation of Primates

Nearly half of all primate species are threatened with extinction as a result of habitat destruction and poaching, and folivorous primates are no exception (Estrada et al. 2017). A fundamental challenge facing primate conservation today is a lack of knowledge regarding the status of endangered populations (Wich and Marshall 2016). Such information is essential in order to develop effective, long-term management plans for conservation. Therefore, understanding the determinants of abundance in folivorous primates is of utmost importance (Chapman and Peres 2001). It has been suggested that the biomass of folivorous primates, especially colobines, is related to the protein-to-fibre ratio of the leaves in their habitats (Chapman et al. 2002). In line with this protein-to-fibre model, the effect of global change on folivorous populations has been examined; a decline in colobine abundance may be explained by the fact that the fibre concentration in their consumed leaves has increased and protein content has decreased over the past 30 years (Rothman et al. 2015).

Contrary to the earlier reports that colobine monkeys are primarily seed-eaters (e.g., Sun et al. 2007), an impact of colobines on their ecosystems as seed dispersers has recently been reported in several taxa such as *Nasalis*, *Presbytis*, *Rhinopithecus* and *Trachypithecus* (Tsuji et al. 2017; Chen et al. 2018; McConkey 2018; Thiry et al. 2019). Even if they are not comparatively efficient endozoochorous and epizoochorous seed dispersers in forest ecosystems, their high abundance and biomass could make them quantitatively significant in seed dispersal (Matsuda et al. 2013).

Available data showing the impact of climate change on food quality and colobine abundance are very limited, and as colobines have been considered as seed dispersers only very recently, the available data testing its impact on their

living-ecosystem are also scarce. Thus, this remains a highly relevant topic that can aid, not only in a basic understanding of colobine population and behavioural ecology, but also in the development of conservation strategies for colobine species. Further work on the importance of colobines in ecological processes (e.g., seed dispersal, nutrient cycling) and their reduced populations on the dynamics of ecosystems is clearly needed.

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