Chapter 3
The Morphophysiological Adaptations of Browsing and Grazing Mammals

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3.1 Introduction

The behaviour, physiology and morphology of animals are the outcome of adaptations to particular ecological niches they occupy or once occupied. Studying the correlation between a given set of characteristics of an ecological niche and the morphological and physiological adaptations of organisms to these characteristics is one of the most basic approaches to comparative biology, and has fuelled scientific interest for generations (Gould 2002). However, current scientific standards cannot be met by mere descriptions of both the characteristics of the niche and the organism, and a (hypothetical) intuitive explanation for the adaptive relevance of the latter; the presence or absence of a characteristic must be demonstrated in sound statistical terms (Hagen 2003)[1] ideally supported by experimental data (from in vivo, in vitro, or model assays) on its adaptive relevance.

In this chapter, we adopt an approach that first presents the relevant characteristics of the ecological niche of the 'grazer' (GR) and of the 'browser' (BR), outlines hypotheses based on these characteristics, and finally addresses examples where such hypotheses have been tested. As we consider that the discussion of morphophysiological differences between GR and BR is still unresolved, subjects of future interest, such as the particular adaptations of mixed feeders, or more elaborate classifications of feeding types (e.g., including frugivores, and differences between grasses, sedges, forbs, herbs, and woody browse), are not considered here. With respect to botanical entities, 'browse' in this chapter refers to herbs, forbs, and leaves and twigs of woody plants.

The terms 'grazer' and 'browser' have been used for a long time to characterise feeding types; however, it was Hofmann and co-workers (Hofmann and Stewart 1972; Hofmann 1973; 1988; 1989; 1991; 1999) who brought them into common use. Partly in connection with the original term 'concentrate selector', which will not be adopted in this chapter (Clauss et al. 2003b; 2003c), the term 'browser' has become synonymous with an organism feeding selectively on relatively easily digestible

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[1] But see recent methodological work in human medicine showing that statistical significance alone cannot be used as an argument to support or falsify a hypothesis (Ioannidis 2005).

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material. Hence, even mites (Siepel and de Ruiter-Dijkman 1993) and carnivorous fish (Lechanteur and Griffiths 2003) have been classified as 'grazers' and 'browsers'. In this chapter, these terms are used strictly in relation to their botanical connotation and are not used as indicators of selectivity. Demment and Longhurst (1987) proposed a classification scheme that demonstrated that there are both selective and unselective species within the GR and BR classes. Selectivity generally decreases with body size (Jarman 1974; Owen-Smith 1988), and differences between feeding type on the one hand and degree of selectivity on the other have been incorporated into a model to explain niche separation (Owen-Smith 1985).

Potential adaptations to browse or grass diets have often been compared to consequences of difference in body mass between species (Hofmann 1989; Gordon and Illius 1994; Gordon and Illius 1996). In this chapter, therefore, body mass is only included as an alternative explanation, but the influence of body mass itself on digestive processes is not reviewed.

3.2 Grass and Browse

Whereas data compilations of animal species have been published in large number (see Sects. 3.3 and 3.5 for references), there is, as far as we are aware, a surprising lack of any systematic evaluation of differences between grasses and browses in terms of their physical and chemical characteristics. In other words, the debate about differences between grazers and browsers is often based on hearsay, as far as the assumed differences between grass and browse are concerned; for example, the often quoted increased amount of grit adhering to grass forage is a conceptual cornerstone of many investigations on the hypsodont dentition of grazers (Fortelius 1985; Janis 1988; Janis and Fortelius 1988; Williams and Kay 2001), but has never been demonstrated quantitatively. Here, we only cite works that generated or at least collated comparative data (even if not statistically testing differences). When considering the literature, we think there is agreement on the forage characteristics (Table 3.1) that are of relevance for the topic of this chapter.

Growth Pattern/Location

These have the potential to influence overall body design and the food selection mechanism.

A1. It is generally assumed that grasses predominate in open landscapes, whereas browse predominates in forests or spatially more structured landscapes.

A2. It is generally assumed that grasses typically grow close to the ground (with evident exceptions such as napier grass), whereas browse grows at different heights (with forbs often at even lower growth levels than surrounding grasses, and woody browse of shrubs and trees mostly above grass level).

Table 3.1 Summary of characteristics of browse and grass used for the generation of predictions of morphophysiological differences between browsers and grazers. The functional relevance (FR) code links these predictions to the following tables. See text for more detailed explanations and references

Subject groups	FR	Characteristic	Browse	Grass
Growth pattern/location	A1	landscape	forests/spatially more structured	open
	A2	growth pattern	at different heights	mostly close to ground
	A3	nutritional homogeneity of a 'bite'	less	more
Chemical composition	B1	protein content	higher (including nitrogenous secondary compounds)	lower
	B2	fibre content	lower but more lignified	higher but less lignified
	B3	pectin content	higher	lower
	B4	secondary compounds	more	less
Physical characteristics	C1	abrasive silica	less	more
	C2	adhering grit	less	more
	C3	resistance to chewing	less	more
	C4	fracture pattern	polygonal	longish fibre-like
	C5	change in specific gravity during fermentation	less	more
Digestion/ fermentation	D1	overall digestibility	lower	higher
	D2	speed of digestion	fast	slow

A3. On the scale of single bites, differences in nutritional quality are more pronounced in browse (Van Soest 1996).

Chemical Composition

These have the potential to influence overall metabolism.

B1. Grass generally contains less protein than browse (Dougall et al. 1964; Owen-Smith 1982; Codron et al. 2007a). The high protein content of browse should be regarded with some caution, since some part of the nitrogen in browse may stem from, or may be bound to, plant secondary compounds (Oftedal 1991). For the calculation of crude protein content, nitrogen content it is generally multiplied by 6.25; in contrast, Milton and Dintzis (1981) suggest that this nitrogen conversion factor should be as low as 4.4 for tropical browse.

B2. Grass contains more fibre, and a greater proportion of this fibre is cellulose, while browse has less total but more lignified fibre (Short et al. 1974; Oldemeyer et al. 1977; Owen-Smith 1982; McDowell et al. 1983; Cork and Foley 1991; Robbins 1993; Van Wieren 1996b; Iason and Van Wieren 1999; Holechek et al. 2004; Hummel et al. 2006; Codron et al. 2007a). These differences are more pronounced if C4 grasses are compared to browse (Caswell et al. 1973). The fact that no difference in fibre content between grass and browse was demonstrated in a comprehensive set of samples of East African forage plants (Dougall et al. 1964) is explained by the inclusion of twigs in the browse analysis and the use of the crude fibre method to estimate fibre content, which can considerably underestimate lignin and hemicellulose content of tropical forage, especially tropical grasses (Van Soest 1975; McCammon-Feldman et al. 1981).

B3. Although few data exist, grass and browse contain comparable low levels of easily digestible carbohydrates, such as sugar and starch (Cork and Foley 1991; Robbins 1993). This is different for pectins, an easily fermentable part of the cell wall, which is much more prominent in the browse cell wall at concentrations of 6–12 % of total forage dry matter (Robbins 1993).

B4. Browse leaves contain secondary plant compounds that can act as feeding deterrents either by poisoning or reducing plant digestibility (Freeland and Janzen 1974; Bryant et al. 1992; Iason and Van Wieren 1999). Common secondary plant compounds such as tannins occur more often in woody browse (80% of taxa) as compared to forbs (15% of taxa; Rhoades and Gates 1976) (see Duncan and Poppi in this book, Chapter 4).

Physical Characteristics

These have the potential to influence adaptations of oral food processing, and might be important drivers of the differentiation of ruminant forestomach morphology.

C1. Grasses contain abrasive silica (Dougall et al. 1964; McNaughton et al. 1985); silica is harder than tooth enamel and thus wears it down (Baker et al. 1959; but see Sanson et al. 2007).

C2. As grasses grow close to the ground, it is assumed that grass forage contains more adhering grit than browse forage, but as stated before, this has not been tested quantitatively. Herbs, typically included in the 'browse' category, should share this characteristic with grasses.

C3. Differences in the masticatory force required to comminute grass/browse have been hypothesised (e.g., Solounias and Dawson-Saunders 1988; Mendoza et al. 2002), but not described. Spalinger et al. (1986) attribute thicker cell walls to grass leaves than to forb and woody browse leaves (while cell walls of twigs were thickest). The grinding of C4 grasses needs distinctively more force than that of C3 grasses (Caswell et al. 1973), possibly due to a greater percentage of bundle sheaths in C4 grasses (Heckathorn et al. 1999).

C4. Differences in fracture patterns of grass and browse have been noted (Spalinger et al. 1986; Kay 1993; Van Wieren 1996a). Several authors have reported more polygonal particles from herbaceous forage leaves and more longish particles from grass leaves (Troelsen and Campbell 1968; Moseley and Jones 1984; Mtengeti et al. 1995). Although empirical studies are lacking, browse is thought to be a more heterogeneous material with different levels of tissue thicknesses and of resistance to breakage, whereas grass is considered more homogenous in this respect. The fibre bundles in grasses are believed to be more evenly distributed and at higher density than in most browse species (Sanson 1989).

C5. Once submitted to fermentation, different forages show different buoyancy characteristics, due to differences in fibre composition, fracture shape, hydration capacity, and bacterial attachment (Martz and Belyea 1986; Lirette et al. 1990; Wattiaux et al. 1992); particles rich in cellulose are expected to change their functional density at a slower rate. Nocek and Kohn (1987) and Bailoni et al. (1998) found that the absolute change in functional specific gravity was greater for grass than for alfalfa hays, suggesting that there may be systematic differences between forages.

Digestion/Fermentation Characteristics

These have the potential to influence overall digestive physiology.

D1. Grass should yield more energy from fermentation per unit forage (Codron et al. 2007a), which explains why both in vivo and in vitro overall digestibility (generally measured as digestibility after fermentation times >24 h) are often found to be higher in grass than in woody browse (Wofford and Holechek 1982; Wilman and Riley 1993; Van Wieren 1996b; Hummel et al. 2006). However, the evidence is equivocal, as some other references give higher digestibilities for woody browse than for grass (Short et al. 1974; Blair et al. 1977; Holechek et al. 2004). All references agree that forbs have a comparatively high digestibility.

D2. Browse is fermented at a faster rate than grass during the initial stages of fermentation (Short et al. 1974; Holechek et al. 2004; Hummel et al. 2006). This characteristic distinction has been well established for alfalfa (higher fermentation rate; lower digestibility) and for grass (lower fermentation rate; higher digestibility; Waldo et al. 1972). The reasons for this might be differences in cell wall structure, but have not been explored in detail. In vivo digestion of different forages confirms the pattern found in vitro (Short 1975). In comparison to C3 grasses and legumes, C4 grasses have some characteristics, such as a more strongly attached epidermis, less loosely arranged mesophyll cells, and a parenchymal bundle sheath, which all may prolong the fermentative process (Wilson 1993), and a slower fermentation rate for a C4 than a C3 grass has been demonstrated by Wilson et al. (1989).

3.3 Predictions

Based on the knowledge of chemical and physical differences between grass and browse, we can put forward hypotheses regarding the morphological adaptations of herbivores to these feeding niches (Table 3.2). In this section, we include visual analyses of data, for example comparative graphs or tables that have not been assessed statistically; such works are considered exploratory or preliminary here. We do not infer such contributions to be of minor relevance; they simply represent an early step in hypothesis testing. Publications that actually test such predictions statistically are not included in this section but appear later in section 3.5 (Results).

It must be noted that the alternative hypothesis to most of the predictions listed here is that there is no influence of feeding type (i. e., browser or grazer) on the respective parameter, but only an influence of body mass and/or phylogenetic descent.

Chemical and Physical Ingesta Properties

B1-B4, C4-C5, D2.[2] It is to be expected that stomach contents of BR and GR differ systematically in their content of chemical, physical, and fermentation characteristics. To our knowledge, no systematic evaluation of protein or fibre content, or of fracture or buoyancy properties, has been performed of the gut contents of herbivores of different feeding types. Owen-Smith (1988) demonstrated correlations between body size and the protein or non-stem fractions in the gut contents of herbivores, thus confirming a principal correlation between body size and selectivity; however, no test for differences between feeding types was performed. It has been suggested that differences in fermentation patterns should be reflected in fermentation rates and their products between BR and GR ruminants (Hofmann 1989), or that differences in content of easily digestible carbohydrates should lead to differences in ruminal pH (Gordon and Illius 1996)—a fact confirmed for a limited number of species by Jones et al. (2001).

Overall Body Design

A1. It is expected that most GR exhibit adaptations in their limb anatomy to living in open habitats, enabling them to use the available open space by increased cursorial activity. Actually, many correlations between postcranial skeleton parameters

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[2] These codes refer to the characteristics of grass and browse outlined in the previous section.

Table 3.2 Summary of predicted morphophysiological differences between grazers and browsers based on the plant characteristics summarised in Table 3.1 [use the functional relevance (FR) code to link plant and animal characteristics]. See text for more detailed explanations and references

Subject groups	FR	Characteristic	Browser	Grazer
Ingesta properties[a]	B1, B2	gut contents nutrient content	higher protein?, lower fibre/ higher lignin	lower protein? higher fibre/ lower lignin
	B3/D2	gut contents volatile fatty acid production rate	higher?	lower?
	C4	gut contents particle pattern	polygonal	longish fibre-like
	C5	gut contents buoancy characteristics	homogeneous	inhomogeneous
Overall body design	A1	limb anatomy	shorter	longer
	A2	adaptations to feeding on the ground	less pronounced: thoracic vertebrae hump, muscles supporting head and skull in grass cropping, paracondylar and glenoid attachment areas, face length	more pronounced: thoracic vertebrae hump, muscles supporting head and skull in grass cropping, paracondylar and glenoid attachment areas, face length
	A3	oral anatomy for selective feeding	more pronounced incisor differentiation, a pointed/narrow incisor arcade, a short muzzle width with long lips, a long mouth opening, pronounced lip muscles	less pronounced incisor differentiation, a square/wide incisor arcade, a long muzzle width with short lips, a short mouth opining, less flexible lip muscles
Metabolism	B1	protein requirements	higher?	lower?
	B4	adaptations against secondary plant compounds	salivary tannin-binding proteins and larger salivary glands, larger livers/increased detoxification capacity	no salivary tannin-binding proteins, smaller livers/ decreased detoxification capacity

(continued)

Table 3.2 (continued)

Subject groups	FR	Characteristic	Browser	Grazer
Dental/buccal morphology	C1, C2	adaptations against abrasion	no hypsodonty; enamel adaptations	hypsodonty; enamel adaptations; consequences of hypsodonty such as deeper mandibles, posterior displacement of orbita
	C3	adaptations to different chewing forces	slender mandible, longer molar tooth row, wider palate, smaller masseter and insertion areas	robust mandible, shorter molar tooth row, narrower palate, larger masseter and insertion areas
	C4	adaptations to different fracture properties	tooth morphology; when consuming grass forage: larger ingesta particles	tooth morphology; when consuming grass forage: smaller ingesta particles
General digestive physiology	D1	daily food intake	higher	lower
	D2	adaptations to differences in digestion kinetics	shorter ingesta retention; on a comparable diet: lower digestibility; lower gut capacity; increased faecal losses (sodium); less cellulolytic activity, less diverse protozoal fauna	longer ingesta retention; on a comparable diet: higher digestibility; greater gut capacity; lower faecal losses; more cellulolytic activity; diverse protozoal fauna
Ruminant forestomach physiology	C4, C5	adaptations to the tendency of forage to stratify	weaker rumen pillars, lower reticular crests, smaller omasa, more viscous saliva, frothy contents, complete rumen papillation, more acid-producing abomasal mucosa	stronger rumen pillars, higher reticular crests, larger omasa, less viscous saliva, stratified contents with fibre mat, fluid layer and gas dome, unpapillated dorsal rumen area, less acid-producing abomasal mucosa

(continued)

Table 3.2 (continued)

Subject groups	FR	Characteristic	Browser	Grazer
Readiness to ingest forage in captivity	C1–C5	problems observed in zoo animals	less acceptance of grass hay	good acceptance of grass hay

[a] Predictions about ingesta properties are made more difficult by the fact that gut contents always consist of a mixture of material recently ingested, of material that has been digested for varying lengths of time, and of symbiotic gut microbes

and habitat have been demonstrated in bovids (Scott 1985, 1987; Kappelman 1988; Köhler 1993; Plummer and Bishop 1994; Kappelmann et al. 1997; DeGusta and Vrba 2003; DeGusta and Vrba 2005a; DeGusta and Vrba 2005b; Mendoza and Palmqvist 2006b). As these represent morphological correlates of habitat rather than diet, they are not dealt with explicitly in this chapter.

A2. In accordance with comparisons using two species (Haschick and Kerley 1996; du Plessis et al. 2004), it is expected that the preferred feeding height of GR is lower than that of BR; consequently, it is expected that GR show adaptations to feeding close to the ground. A lower angle between braincase and the facial cranium should be a positional adaptation to ground feeding. The peak of the hump of the thoracic vertebrae should be correlated with the preferred feeding height, with a tall hump close to the head being advantageous for ground-level feeding (increases the moment arm of the nuchal musculature; Guthrie 1990); however, results from analyses on this hump so far are equivocal (Spencer 1995), which could be due to the fact that those browsers feeding on herbs/forbs would, by necessity, also have to feed close to the ground. Muscles supporting head and skull movements in grass cropping should be more pronounced in GR with accordingly more pronounced attachment areas (paracondlyar and glenoid). A longer face could serve to keep the eyes away from the grass, which might protect them (Janis 1995), help to maintain good visibility for predator detection during feeding (Gentry 1980), and/or enhance moment arms of the head and mandible for more efficient cropping and mastication. An interesting potential example of a skeletal feeding height adaptation is the decreasing length of the metatarsus in Sivatheres with increasing proportion of grass in their diet (Cerling et al. 2005).

A3. BR are expected to show adaptations for a more selective feeding, whereas GR are expected to show adaptations for a more unselective food intake. Browsers are expected to have a higher dental incisor index (i.e., a more pronounced size difference between the individual incisor teeth and the canine teeth; Boué 1970). BR are expected to have a lower muzzle width, a more pointed and narrower incisor arcade than GR, which have more square incisor arcades (Boué 1970; Bell 1971; Owen-Smith 1982; Bunnell and Gillingham 1985; Gordon and Illius 1988; Solounias et al. 1988; Solounias and Moelleken 1993). GR are assumed to have a small mouth opening and short lips, whereas BR should have a larger mouth opening and longer lips (Hofmann 1988). As BR are thought to need more flexible lips, a larger lip muscle attachment area has been suggested in BR (Solounias and Dawson-Saunders 1988), and a seemingly larger size of the infraorbital and stylomastoidal foramina in BR ruminants has been interpreted as indicative of more innervation of the lip muscles compared to GR (Solounias and Moelleken 1999).

Metabolism

B1. In the zoo animal literature, it has been proposed that BR have higher protein requirements for maintenance than GR. No statistical treatment of this question is known to us. However, comparisons of experimentally established protein maintenance requirements between BR and GR species (collated in Robbins 1993; Clauss et al. 2003b) do not suggest any relevant systematic difference between the feeding types.

B2. A particular adaptation of GR to the digestion of cellulose would be expected. This is subsumed under the prediction D2, as fibre content cannot be separated from fermentation characteristics.

B4. In order to counteract plant secondary compounds, it has been suggested that BR produce salivary proteins that bind to these compounds. See Clauss (2003) and Shimada (2006) for reviews of species in which such proteins have been demonstrated; however, the number of species investigated thus far makes a statistical comparison between BR and GR unfeasible. Supposedly larger salivary glands of BR ruminants (Kay et al. 1980; Kay 1987b; Hofmann 1988) have been considered to be a morphological correlate of a high production of these salivary proteins (Robbins et al. 1995). The BR that has been demonstrated to deviate from the general ruminant pattern, the greater kudu (*Tragelaphus strepsiceros*; Robbins et al. 1995), has been noted to suffer from die-offs due to tannin poisoning (Van Hoven 1991), although even kudus can include plants in their diet that are known to be poisonous for livestock (Brynard and Pienaar 1960). A larger liver, used for secondary plant compound detoxification, has been postulated in BR ruminants (Hofmann 1988; Duncan et al. 1998) and in the black rhinoceros (*Diceros bicornis*), a browser (Kock and Garnier 1993), as compared to GR ruminants and GR rhinos. It has been demonstrated, in pair-wise comparisons in rodents, macropods, and ruminants, that BR are less affected by dietary secondary compounds than GR (Iason and Palo 1991; Robbins et al. 1991; Hagerman et al. 1992; McArthur and Sanson 1993). Statistical treatments of these topics for a large range of species is still required.

Dental and Buccal Morphology

C1, C2. Silica is harder than enamel, and a grass diet should wear down teeth faster than does browse. Therefore, significant differences between GR and BR in enamel microwear or molar wear rates (Solounias et al. 1994; Solounias and

Semprebon 2002) are expected. As molar wear is a function of both attrition (tooth-to-tooth contact, which maintains sharp edges) and abrasion (tooth to food contact, which produces blunt edges), differences in the 'mesowear' pattern [the macroscopically evaluated shape and reliefs of the cusps of selected teeth first introduced by Fortelius and Solounias (2000)] between feeding types are also expected. Differences in mesowear patterns between upper and lower molars in different feeding types indicate different morphological adaptations (Franz-Oftedaal and Kaiser 2003; Kaiser and Fortelius 2003). Hypsodonty (as an adaptation to increased tooth wear due to abrasion and maybe increased attrition; C.3) has been observed in many GR groups such as marsupials, rodents, lagomorphs, and ungulates (Simpson 1953; Fortelius 1985; Janis and Fortelius 1988). Experimental work on the influence of crown height on survival is summarised in Williams and Kay (2001). Hypsodonty will have other consequences for cranial morphology, such as deeper mandibles to accommodate the hypsodont teeth (Vrba 1978). As a secondary change due to hypsodonty and the increased space requirement for the higher maxillary molars (and the masseteric insertion areas; C.3), it is assumed that in GR the orbita needs to be positioned more posteriorly than in BR (Solounias et al. 1995). This will also lead to an elongation of the whole skull. In a comparison of three macropod species, enamel hardness was greater in the GR than in the BR species (Palamara et al. 1984).

C3. The purportedly tougher consistency of grasses and higher chewing pressure needed by GR to break down grass would require a more robust mandible structure (that also accommodates hypsodont teeth; C1, C2). A possible mechanism to withstand increasing pressure/torsional forces in GR ruminants is the reduction of the premolar tooth row length (Greaves 1991), and a reduction of palatal width. In perissodactyls, premolar tooth reduction does not occur, perhaps due to the requirement for increased food intake (Janis and Constable 1993). A greater masseter muscle mass, and accordingly larger masseter insertion surfaces, are assumed for GR, which is thought to reflect the higher masticatory forces required to grind grass material (Turnbull 1970; Stöckmann 1979; Axmacher and Hofmann 1988). A larger masseter, requiring more nerve tissue for innervation, has been hypothesised to be the reason for seemingly larger foramina ovale (through which the masseter nerves pass) in GR ruminants (Solounias and Moelleken 1999).

C4. Different fracture properties of browse and grass should be reflected in differences in tooth occlusal surface morphology (Fortelius 1985; Sanson 2006); and these differences in tooth morphology should be reflected in differences in ingesta particle reduction between species on a similar food source (Lentle et al. 2003c).

General Digestive Physiology

D1. Given the higher potential digestibility of grass, one would either expect BR to have lower basal metabolic rates at similar intake levels, or similar BMRs at higher intake levels, or GR to have lower BMRs at relatively low intake levels.

The BMR data available for ruminants (Williams et al. 2001) does not suggest a systematic difference in BMR between the feeding types, and hence it would be expected that BR have higher intakes.

D2. Optimal digestion theory (Sibly 1981) predicts that animals adapted to a forage that yields energy and nutrients quickly would have short retention times, and those that ingest a forage that yields energy and nutrients more slowly would have longer retention times. This has been postulated for ruminants (Hanley 1982; Kay 1987a; Hofmann 1989; Clauss and Lechner-Doll 2001; Behrend et al. 2004; Hummel et al. 2005a), however, a comprehensive dataset based on comparable measurements is still lacking.

Differences in retention time would have far-reaching consequences: on comparable diets, BR should achieve lower digestion coefficients than GR (for ruminants: Owen-Smith 1982; Prins et al. 1983; Demment and Longhurst 1987). A higher food intake in BR, due to the supposedly shorter passage times, has been suggested (Owen-Smith 1982; Baker and Hobbs 1987; Prins and Kreulen 1991). Forage that ferments faster and is retained shorter should also be ingested in shorter time intervals, and a higher feeding bout frequency has been suggested in browsing ruminants (Hofmann 1989; Hummel et al. 2006). A combination of higher food intake and lower digestibility should theoretically result in a comparatively higher faecal output in BR, which could be expected to have further consequences. For example, Robbins (1993) states that sodium losses are a function of faecal bulk, and higher faecal sodium losses have been observed in the browsing black rhinoceros (*Diceros bicornis*) than in the domestic horse (Clauss et al. 2006a).

Cellulolytic activity in the rumen of BR is expected to be lower than that of GR (Prins et al. 1984; Deutsch et al. 1998). GR have a more diverse protozoal fauna, whereas BR protozoa are mostly *Entodinium sp.*; as these are particularly fast-growing ciliates, it has been suggested that other protozoa cannot establish viable populations in the reticulorumen (RR) of BR (Prins et al. 1984; Dehority 1995; Dehority et al. 1999; Clauss and Lechner-Doll 2001; Dehority and Odenyo 2003; Behrend et al. 2004). Other parameters indicative of shorter ingesta retention times (Clauss and Lechner-Doll 2001; Behrend et al. 2004) are a lower degree of unsaturated fatty acid hydrogenation in the RR, a greater number of glucose transporters, and a higher amylase activity in the small intestine of BR,[3] as well as larger faecal particles in BR. In order to maintain intake levels whilst still having prolonged ingesta retention in the rumen, GR should have more capacious rumens (Prins and Geelen 1971; Giesecke and Van

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[3] The hypothesis that BR maintain a functional reticular groove throughout their adult lives (Hofmann 1989) has not been tested directly (Ditchkoff 2000); however, a comparison of fluid retention data from two different trials on roe deer (*Capreolus capreolus*) indicates that bypass of soluble substances from the rumen via the reticular groove is probably not a quantitative factor, at least in this species (Behrend et al. 2004).

Gylswyk 1975; Drescher-Kaden 1976; Hoppe 1977; Kay et al. 1980; Owen-Smith 1982; Bunnell and Gillingham 1985; Van Soest 1994). It has been suggested that BR have more capacious hindguts (Hofmann 1988), but this view has recently been modified (Clauss et al. 2003a; Clauss et al. 2004).

Macropods

C1C3. Macropods have been classified in feeding types based on their dental morphology (Sanson 1989). Macropod teeth have a crushing action over a relatively large occlusal contact area in BR, with dentine basins making up a large percentage of this surface area. As macropods have evolved to feed more on grass, the area of occlusal contact has been decreased by increasing the complexity of the enamel ridges and increasing the curvature of the tooth row (Janis and Fortelius 1988; Sanson 1989; Lentle et al. 2003b; Lentle et al. 2003a). The macropod feeding type classification of Sanson (1989) was tested for two macropod species by Sprent and McArthur (2002); the results were in accord with Sanson's prediction. Differences in ingesta particle size distribution between four macropod species, tested in sets of both free-ranging and captive animals, support the notion that teeth of GR are more suited to the fine-grinding of grass material (Lentle et al. 2003c).

C4-C5. It has been postulated that grazing macropods have a lower proportion of the sacciform relative to the tubiform forestomach (Freudenberger et al. 1989). This could be due to the fact that macropods do not ruminate, and as a result, ingesta stratification in a larger sacciform forestomach would not be beneficial to GR. At the same time, comparisons indicate that, in GR macropods, the length of the large intestine is greater than in BR, indicating additional fermentation of the slower-fermenting grasses in this site (Freudenberger et al. 1989).

Ruminant Forestomach Morphophysiology[4]

C4-C5. Recently, it has been hypothesised that a key to the understanding of ruminant forestomach physiology is the presence or absence of a stratification of RR contents (Clauss and Lechner-Doll 2001; Clauss et al. 2001, 2002, 2003c).

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[4] We feel that a major basis of the discussion on potential differences in digestive morphophysiology between GR and BR ruminants has been to confirm or refute Hofmann's original observations and hypotheses, rather than necessarily to understand the functional relevance of his findings. Here, we present a new, complex interpretation of ruminant forestomach physiology; this is not a "refutation" of Hofmann's hypotheses but a refinement and readjustment, based on his anatomical observations, the validity of which is not drawn into question (but should be submitted to statistical evaluation).

Physical and chemical characteristics of grass are thought to enhance the development of this stratification, with particle separation occurring according to flotation/sedimentation, and a 'fibre raft' or 'fibre mat' on top of a liquid layer; to these, the animal has to adapt, for example with stronger rumen pillars (to work against the tough consistency of the 'mat'), with deeper reticular honeycomb cells (traps for the sedimenting particles in the liquid phase), or larger omasa (for water re-absorption from the liquid outflow out of the RR). As the stratification enhances particle retention and, hence, fibre digestion (Beaumont and Deswysen 1991; Lechner-Doll et al. 1991), adaptations encouraging stratification would be expected to have evolved in GR. The most controversial part of the traditional concept of wild ruminant RR physiology is that the larger salivary glands of BR (Hofmann 1988) are assumed to translate into a higher saliva production rate and, hence, a higher fluid throughput through the RR. If this was the case, then the comparatively smaller omasa of BR (Hofmann 1988; Clauss et al. 206c) would not make sense; the primary function of the omasum is fluid re-absorption. If fluid throughput was particularly high in BR, then they, not GR, should have the larger omasa. The concept of higher salivary flow rate in BR was challenged by Robbins et al. (1995) on the basis of a three-species comparison. It has been proposed that the difference between particle and fluid retention in the RR is a distinguishing characteristic of the different feeding types, with the difference between the phases being large in GR—indicative of ingesta stratification—and small in BR (Clauss and Lechner-Doll 2001; Hummel et al. 2005a). However, the question whether this difference stemmed from longer particle or shorter fluid retention times in GR, or both, has not been addressed comprehensively to date. Comparisons between the few species on which data exist indicate that GR have both a shorter fluid, and a longer particle retention time in the RR than do BR (Clauss et al. 2006c). We propose that the production of a large amount of non-viscous saliva is a particular adaptation of GR and supports the development of RR contents stratification, whereas the more viscous saliva of BR delays any separation of ingesta particles by flotation/sedimentation. Thus, the size of the salivary glands is probably not correlated with saliva production but with saliva protein content (c.f. B4) and hence viscosity (Robbins et al. 1995). Results of Jones et al. (2001) who found that several browsers had a higher dry matter content in rumen fluid as compared to grazers supports the concept of a higher fluid viscosity in browsers. In a low-viscosity medium, the fermentation gases, carbon dioxide and methane, can easily rise and gather in the dorsal RR. Rumen papillae development is stimulated by the presence of volatile fatty acids (in particular, of butyrate) (Warner et al. 1956). The continuous presence of a gas dome of CO_2 and methane in the dorsal rumen will prevent any significant concentration of volatile fatty acids in this region, leading to unpapillated dorsal rumen surfaces in GR (Hofmann 1973). In a more viscous medium, fermentation gases cannot dissociate from food particles to rise and gather in the dorsal rumen as easily, which results in the typical 'frothy' appearance of BR RR contents (Clauss et al. 2001) and an even RR papillation (Hofmann 1973). The escape of a more a viscous ingesta that traps CO_2 into the abomasum would also explain why browsers have a thicker layer of acid-producing abomasal mucosa (Hofmann 1988), inasmuch as the presence of CO_2 would increase the buffering capacity of the ingesta.

Captive Animals: Readiness to Ingest Forage

Based both on dental and, in the case of ruminants, forestomach characteristics, GR should have less problems in eating browse than BR in eating grass (Clauss et al. 2003c). This hypothesis finds support in reports for captive wild ruminants (Clauss et al. 2003b), for macropods (Lentle et al. 2003c), suids (Leus and MacDonald 1997), and from the well-known reluctance of captive tapirs to ingest grass hay (Foose 1982). Captive BR ruminants ingest less hay and have a higher incidence of rumen acidosis (due to a lack of fibre) than GR ruminants (Clauss et al. 2003b). Commercially available pelleted feeds for captive wild herbivores in general or GR in particular have a distinctively lower fibre content than diets designed especially for BR, again indicating that one cannot rely on a sufficient fibre intake via hay consumption by BR (Clauss and Dierenfeld 2007). Due to the high abrasiveness that characterizes the diets of both free-ranging grazers and that fed to captive animals in general, the tooth wear pattern of captive browsers resembles that of free-ranging grazers (Clauss et al. 2007a).

3.4 Testing the Hypotheses

Testing these hypotheses involves problems that have, historically, been addressed in different ways in different publications. The following discussion raises issues about the approaches used to test for morphophysiological adaptations to diet in herbivores.

Body Mass

Body mass (BM) is the single most influential factor on the absolute size of any anatomical, and of most (but not necessarily all) physiological parameters (Schmidt-Nielsen 1984; Peters 1986; Calder 1996). Therefore, the inclusion of BM in statistical evaluations is self-evident. Ideally, datasets should cover similar BM ranges for all feeding types investigated. On average, grazing ruminants are larger than browsing ruminants (Bell 1971; Case 1979; Bodmer 1990; Van Wieren 1996b; Pérez-Barbería and Gordon 2001). However, there is either no correlation (Van Wieren 1996b; Clauss et al. 2003c; Sponheimer et al. 2003), or it is very weak (Gagnon and Chew 2000), between BM and the proportion of grass in the natural diet of ruminants. This is because browsers are found across the body size range (Sponheimer et al. 2003). The largest extant ruminant, the giraffe (*Giraffa camelopardalis*), is a browser, the largest marsupial herbivores were browsers (Johnson and Prideaux 2004), and the largest known terrestrial mammalian herbivore ever, the Indricotherium (Fortelius and Kappelman 1993), was also a browser; extensive grasslands did not exist when this species inhabited the earth (Janis 1993). Large BM, therefore, does not preclude a browsing lifestyle (Hofmann 1989).

The question of whether there are different upper and lower body size thresholds for the feasibility of grazing or browsing in ruminants has been addressed by Demment and Van Soest (1985) and by Clauss et al. (2003a). Assuming feeding type independent general relationships between body mass and forestomach capacity, and between body mass and ingesta retention, Demment and Van Soest (1985) demonstrated that, theoretically, grazing by ruminants is feasible at greater body masses than browsing; using, in contrast, feeding type specific relationships between body mass and forestomach capacity and ingesta retention, Clauss et al. (2003a) demonstrated that browsing is theoretically feasible at larger body masses—a result seemingly in better accord with the extant and fossil ruminant record.

Two examples illustrate the importance of choosing a specific BM value when evaluating morphological and physiological data: Hofmann (1973) gives data on the length of the curvature of the omasum (which he claims is larger in GR than in BR) for the giraffe (52–71 cm) and the African buffalo (*Syncerus caffer*) (72 cm). The BM data given in Hofmann (1973) are derived from the literature (giraffe, 750 kg; buffalo, a range of 447–751 kg). Should one chose to compare both measurements on the basis of the maximal BM (750 vs. 752 kg), hardly any difference between the species would be evident; should one chose to use the averages/medians of the given BM data (750 kg vs. 599 kg), then the GR buffalo would be assumed to display a relatively larger omasum. Another example is the greater kudu in Hofmann's (1973) dataset. The BM range, again taken from the literature, is 170–257 kg. However, the handwritten notes in Hofmann's archive record estimated BM of the animals investigated to range from 220 to 350 kg (M. Clauss, pers. obs.). These actual BM data would link the anatomical measurements to a higher average BM, thus reinforcing potential differences between the feeding types. The importance of measurements of morphophysiological traits and BM from the same individuals, therefore, cannot be overemphasised. In studies that use measurements on museum skeleton specimens (for which live BM data is usually missing), the use of a parameter that can be measured on the museum specimen and is known to correlate closely with BM or BM-independent ratios are alternatives (for example Janis 1988; Spencer 1995; Archer and Sanson 2002).

Definition of Feeding Type

In order to compare adaptations of different species, the species have to be classified according to niches that are relevant to the adaptations under investigation. This has mostly been done by allocating feeding type labels, such as 'BR' or 'GR', as discrete variables. The available information on diet composition on which such a classification is based differs between species (Gagnon and Chew 2000). A common practice has been to collect published data on the botanical composition of a species' diet, calculate an average value for the different reports, and then use pre-defined thresholds to allocate a feeding type. These thresholds have not been used consistently in the literature; in particular, some publications allocate species with >75 % of the respective forage to the BR or GR category (Pérez-Barbería and Gordon 1999; Pérez-Barbería et al. 2001a; Mendoza et al. 2002), whereas other publications reserve these categories only for species consuming >90 % of the respective forage (Janis 1990; Pérez-Barbería et al. 2001b). The impact of the choice of allocation of species to feeding types is demonstrated for example by Gordon and Illius (1994), who showed that results differed depending on the classification used. A more consistent approach (Janis 1995; Clauss et al. 2003c; Sponheimer et al. 2003; Pérez-Barbería et al. 2004) does not use a discrete variable, but uses the percentage of grass and/or browse in the natural diet as a continuous variable. But while such an approach overcomes the need to make arbitrary 'threshold decisions', it should be remembered that the information contained in such a continuous variable is not perfect since there can be enormous geographical and seasonal variation in diet composition in some species (Owen-Smith 1997). An important limitation of the description of 'natural' diets is explained by Sprent and McArthur (2002): in any natural setting, the 'typical' forage preference pattern is evidently modified by the available forage. Ideally, a selected diet should always be expressed in terms of the available diet.

It should be borne in mind that allocating feeding types on the basis of actual observations does not provide full information on the nutritional adaptation of species. Although it is generally viewed that species diversification followed the sequence of BR/closed habitat, mixed feeder, GR/open habitat (Pérez-Barbería et al. 2001b), the reverse has been suggested or noted occasionally for extant and extinct species (Solounias and Dawson-Saunders 1988; Thenius 1992; Cerling et al. 1999; MacFadden et al. 1999). The morphology of species that are in a transition/regression state in this respect may not be completely correlated with dietary behaviour yet. The different evolutionary directions that led species to their present state can potentially make convergent evolutionary traits more difficult to discern (Gould 2002).

Phylogenetic Descendence

If values for individual species are used in statistical tests, these values cannot be viewed as independent because the species are phylogenetically related (Harvey and Pagel 1991; Martins and Hansen 1996). In recent years, phylogenetic control in statistical tests has become standard procedure for evaluating differences between or correlations with feeding types (c.f. the work of Pérez-Barberìa et al.). Published results can be classified into those that do not remove phylogenetic effects in the analysis (generally earlier studies) and those that do. This leads to the dilemma that results from earlier studies cannot be quoted with confidence, but direct replication of tests are rarely performed on the same datasets.

The method of phylogenetic control has been criticised (Westoby et al. 1995), but this discussion shall not be reviewed here. The most informative approach is to conduct two analyses, without and with phylogenetic control. If, for example, a certain measure shows a difference between feeding types, after controlling for body mass alone, this indicates that it represents either (1) a case of convergent evolution between lineages or (2) evolution within a certain lineage that dominates the dataset. If, in a second step, no difference between feeding types is found, when phylogeny is controlled for, then the hypothesis of convergent evolution between lineages can be rejected, but not necessarily the hypothesis of evolution within a certain lineage, nor the adaptive value of the trait as such. The rejection of the hypothesis of convergent evolution should not be confused with a rejection of the hypothesis of adaptive value, which can only be tested experimentally.

Two important choices have to be made when phylogenetic control is applied. The phylogenetic tree should, ideally, be based on characters unrelated to the character that is submitted to the test. In this respect, one should, for example, note that many of the dental characters understood to be adaptations to feeding niches (Janis 1990) have also been used to establish phylogenetic relations in ungulates (Janis and Scott 1987). The case of the more recently discovered mammalian taxonomic clades of the Afrotheria, Laurasiatheria, and Euarchontoglires implies a widespread accumulation of homoplasious morphological features in various placental clades and thus exemplifies the difficulty of basing phylogenetic trees on morphological characters (Robinson and Seiffert 2004). The other choice refers to the spectrum of species included in the analysis, that is, the level at which convergent evolution is to be assessed. On the one hand, if there is some trait showing convergent evolution within the ruminants, then this trait will be more difficult to detect in a dataset comprising only bovids than in a dataset that comprises both bovids and cervids. On the other hand, an expansion of the species dataset beyond certain phylogenetic borders may appear unreasonable. When rumen capacity or rumination activity is compared between feeding types, only ruminants (and maybe camelids) will be included but not other ungulates. Similarly, ingesta retention should be analysed separately for ruminants and hindgut fermenters, due to the differences in digestive physiology (Illius and Gordon 1992). Other examples include systematic differences in cranial morphology. For example, in perissodactyls, the lower premolar row increases in length in grazing species whereas it decreases in grazing ruminants and macropods (Janis 1990; Mendoza et al. 2002), and grazing horses have relatively smaller muzzles than corresponding grazing ruminants (Janis and Ehrhardt 1988). Therefore, inclusion of phylogenetically distant groups in one analysis might yield different results from an analysis within each of these groups; in this respect, the finding that a parameter shows no convergent evolution in GR or BR *ungulates* does not falsify the finding that such convergent evolution occurs within GR or BR *ruminants*. This latter question would have to be addressed by an analysis using only ruminant data. The power of a variable to predict the feeding type correctly, hence, usually increases as the taxonomic level is narrowed from ungulates to either artiodactyls or perissodactyls (Janis 1995).

Statistical Procedure

Generally one can distinguish uni- or bivariate statistics (testing one trait, for example a ratio, or two if control for BM is included, between feeding types), or a multivariate approach. The advantage of a multivariate approach is that a number of characteristics are included that will, each and together, contribute to the adaptation of a feeding type. A potential disadvantage of a multivariate approach might be the temptation to include as many data as possible without giving attention to the functional relevance of the different parameters. In this respect, multivariate analysis can be considered to be exploratory, unless it is followed or preceded by further detailed investigations (Spencer 1995; Archer and Sanson 2002). In the selection of data for a multivariate approach, partly repetitive information—for example, both volumetric and linear measurements of the same organ, or both the length of the molar tooth row and the length of the individual molars—has either been included (Pérez-Barbería et al. 2001a) or excluded (Mendoza et al. 2002).

Parameter Choice and Measurement Resolution

All previous considerations notwithstanding, the most important prerequisite for a meaningful analysis is that the parameters investigated have a functional relevance, and that they are measured with appropriate resolution so that meaningful differences can be detected. The necessary degree of resolution is intuitively more evident in anatomical than in physiological studies. No one would conceive of comparing incisor breadths measured to the closest 0.1 meter. Yet, for example, the method employed by Foose (1982) for the estimation of ingesta retention (using one or two pooled faecal samples per day) can be expected to be of sufficient resolution to differentiate between hindgut and foregut fermenters (the aim of Foose's study), but hardly so between browsers and grazers of either category. If data compilations from different publications are used for an analysis, the consistency of the methods applied, therefore, is of prime importance; an additional solution is to include data source as a random variation in the analysis (Pérez-Barbería et al. 2004). In many studies, the functional significance of parameters tested has not only *not* been proven by experimentation, but is sometimes not even defined in logical terms. For example, the concept stated by Hofmann (1988) and repeated many times by others that 'openings' in the ruminant forestomach such as the ostium intraruminale or the ostium ruminoreticulare, the diameters of which are by magnitudes greater than the particles that leave the rumen, should have any influence on ingesta retention is not self-evident and would have to be backed by engineering models (or rapidly dismissed).

3.5 Results

In this section, publications are summarised that generated or collated comparative data and submitted these data to statistical tests for differences between the feeding types. The individual morphological and physiological traits are listed in tables 3.3–5, and comprehensive multivariate analyses are explained in the text. In general, the lack of phylogenetically controlled studies on different taxonomic groups does not allow definite conclusions.

Macropods

Results of morphological craniodental comparisons within the macropods are given in Table 3.3. No phylogenetically controlled approach has been used thus far. Some, but not all of the predictions regarding craniodental design seem to be met. As with ruminants, GR macropods also show a shorter premolar row length, but have smaller muzzles than do BR macropods.

Table 3.3 Statistical tests for craniodental differences between grazing (GR) and browsing (BR) macropods. From (Janis 1990); $n = 52$, original data (not given), discrete feeding type allocation. FR = functional relevance, FT = feeding types (significance without/with phylogenetic control). BM = body mass

Parameter	FR	FT	Direction
Basicranial angle	A2	*/-	GR < BR
Anterior jaw length	A2	ns/-	
Width of central incisor	A3	ns/-	
Width of lateral incisor	A3	*/-	GR > BR
Muzzle width	A3	*/-	GR < BR
Hypsodonty index	C1-C2	*/-	GR > BR
Distance orbita tooth row	C1-C2	*/-	GR > BR
Lower premolar row length	C3	*/-	GR < BR
Lower molar row length	C3	ns/-	
Depth of mandibular angle	C3	ns/-	
Maximum width of mandibular angle	C3	ns/-	
Length of coronoid process	C3	ns/-	
Length of masseteric fossa	C3	ns/-	
Palatal width	C3	ns/-	

Rodents

The only analysis pertaining to rodents indicates that GR have a higher hypsodonty index (after phylogenetic control) than do BR (Williams and Kay 2001).

Ungulates

Results of uni- and bivariate analyses are given in Table 3.4. Additionally, a multivariate analysis (without phylogenetic control) of a set of 22 craniodental variables in 115 species (Mendoza et al. 2002) indicated that differences exist between the feeding types. As in macropods and rodents, hypsodonty is identified as a primary distinction between BR and GR, being greater in GR than in BR. For several parameters (skull length, muzzle width, occlusal surface, tooth row lengths), opposing trends between artiodactyls and perissodactyls might have led to nonsignificant results in the ungulate comparison. Similarly, masseter parameters could be significant simply because equids—all GR—have larger masseter muscles than ruminants (Turnbull 1970). Thus, phylogenetic control leaves only very few parameters of convergent evolution within the ungulates, either indicating that no differences between feeding types exist, or that they should be looked for at lower taxonomic levels. Recently, in an explorative analysis including phylogenetic control, without a specific hypothesis, Pérez-Barbería and Gordon (2005) did not find any relevant correlation between feeding type and brain size in ungulates.

Perissodactyls

The dental anatomy of browsing rhinoceroses (*D. bicornis, Dicerorhinus sumatrensis*) differs distinctively from that of the grazing *Ceratotherium simum* but not *Rhinoceros unicornis* (Palmqvist et al. 2003); similarly, production of salivary tannin-binding proteins differ between *C.simum* on one hand, and *D. bicornis* and *R. unicornis* on the other (Clauss et al. 2005b). This could indicate that *R. unicornis* ingests more browse or fruit than previously reported, or that this species has switched to a grass-dominated diet recently. There is a significant difference in tooth sharpness, with particularly blunt tips in the grazing *C. simum* as compared to *D. bicornis* (Popowics and Fortelius 1997). It has been demonstrated that ingesta retention in the browsing *D. bicornis* was shorter than expected for its body mass when compared to grazing rhinoceroses and equids (Clauss et al. 2005a). Digestion coefficients achieved by the two browsing rhinoceros species *D. bicornis* and *D. sumatrensis* are lower than those of grazing rhinoceroses at comparable levels of dietary fibre content (Clauss et al. 2006b).

Table 3.4 Statistical tests for morphological differences between grazing (GR) and browsing (BR) ungulates. FR = functional relevance, *n* = number of species, dg = data given (yes/no), od = original data (yes/no), FTC = feeding-type classification (d = discrete; c = continuous), FT = difference between grazers/browsers significant without/with phylogenetic control, BM = correlation with body mass significant without/with phylogenetic control. * = significant, ns = not significant, ds = difference in slope, - = not done

Parameter	FR	*n*	dg	od	FTC	FT	BM	Direction	Source
Basicranial angle	A2	136	n	y	d	*/-		GR < BR	(Janis 1990)
Total skull length	A2, C1, C2	136	n	y	d	ns[a]/-			(Janis 1990)
Posterior skull length	A2, C1, C2	136	n	y	d	*/-		GR > BR	(Janis 1990)
Rel. muzzle width (palate/muzzle)	A3	95	y	y	d	*/-		GR > BR	(Janis and Ehrhardt 1988)
Muzzle width	A3	136	n	y	d	ns[a]/-			(Janis 1990)
Muzzle width	A3	104	y	n	d	*/ns	*/*		(Pérez-Barbería and Gordon 2001)
Width central incisor	A3	136	n	y	d	*/-		GR > BR	(Janis 1990)
Width lateral incisor	A3	136	n	y	d	*/-		GR > BR	(Janis 1990)
Rel. incisor width (I1/I3)	A3	70	y	y	d	*/-		GR < BR	(Janis and Ehrhardt 1988)
Rel. incisor width (I1/I3)	A3	66	y	n	d	ns/ns	*/*		(Pérez-Barbería and Gordon 2001)
Incisor protrusion	A3	25	y	n	d	*/ns	*/*		(Pérez-Barbería and Gordon 2001)
Hypsodonty index	C1, C2	128	y	y	d	*/-		GR > BR	(Janis 1988)
Hypsodonty index	C1, C2	136	n	y	d	*/-		GR > BR	(Janis 1990)
Hypsodonty index	C1, C2	79	n	y	c	*/-		GR > BR	(Janis 1995)
Hypsodonty index	C1, C2	57	n	n	d	-/*		GR > BR	(Williams and Kay 2001)
Hypsodonty index	C1, C2	19	n	n	c	*/-		GR > BR	(Codron et al. 2007b)
M3 height	C1, C2	121[b]	y	y	d	*/-	*/-	GR > BR	(Janis 1988)
M3 height	C1, C2	113	y	n	d	*/*	*/*	GR > BR	(Pérez-Barbería and Gordon 2001)

M3 volume	C1, C2	121	y	y	d	*/-	*/-	GR > BR	(Janis 1988)
M3 volume	C1, C2	113	y	n	d	(ds)	*/*	GR > BR	(Pérez-Barbería and Gordon 2001)
Distance orbita tooth row	C1-C2	136	n	y	d	*/-		GR > BR	(Janis 1990)
Postcanine tooth row volume	C1, C3	121	y	y	d	*/-	*/-	GR > BR	(Janis 1988)
Molar row volume	C1, C3	113	y	n	d	*/*	*/*	GR > BR	(Pérez-Barbería and Gordon 2001)
Occlusal surface	C3	92	y	n	d	ns[a]/ns	*/*		(Pérez-Barbería and Gordon 2001)
Lower M2 area	C3	136	n	y	d	*/-		GR < BR	(Janis 1990)
Depth mandibular angle	C3	136	n	y	d	*/-		GR > BR	(Janis 1990)
Max. width mandibular angle	C3	136	n	y	d	*/-		GR > BR	(Janis 1990)
Length coronoid process	C3	136	n	y	d	*/-		GR > BR	(Janis 1990)
Length masseteric fossa	C3	136	n	y	d	*/-		GR > BR	(Janis 1990)
Palatal width	C3	136	n	y	d	ns/-			(Janis 1990)
L. premol. tooth row length	C3	136	n	y	d	ns[a]/-			(Janis 1990)
L. molar tooth row length	C3	136	n	y	d	ns[a]/-			(Janis 1990)
17 jaw and 4 skull traits, including most of the parameters listed above [except those used in Pérez-Barbería and Gordon (2001)]		94	n	y	d	*/ns			(Pérez-Barbería and Gordon 1999)

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[a] opposing trends in artiodactyls and equids

[b] excluding equids from the dataset

While extant equids are uniformly classified as GR, there is a large number of BR equids in the fossil record (MacFadden 1992). The feeding type of fossil horses is generally determined by a combination of isotope, hypsodonty, and microwear data (MacFadden et al. 1999). In theory, it would be feasible to compare feeding types classified in this manner for other osteological measurements. MacFadden (1992, pp 241–242) gives the example of an equid with a low hypsodonty index and a pointed muzzle shape as would be expected of a BR, and another one of an equid with a high hypsodonty index and a broad muzzle as would be expected of a GR. However, a quantitative approach to such correlations in the fossil record is lacking.

Proboscids

Extant elephants are intermediate feeders with a preference for browse, but isotopic investigations show that both lineages were once grazers and are in a transition back to browsing (Cerling et al. 1999). Isotopic evidence suggests that the Asian elephant (*Elephas maximus*) might ingest a higher proportion of grass than the African elephant (*Loxodonta africana*). This difference is confirmed by microwear results (Solounias and Semprebon 2002). The differences in molar structure between the two species (with *L. africana* having less enamel ridges than *E. maximus*; Maglio 1973) could be interpreted as a higher degree of adaptation for grass forage in *E. maximus*. Elephants differ in their digestive physiology from other ungulates due to their very short retention times and low digestion coefficients (Clauss et al. 2003d; Loehlein et al. 2003). Hackenberger (1987) found significantly longer ingesta retention times in *E. maximus* compared to *L.africana* and correspondingly higher digestion coefficients for *E. maximus* than *L.africana* when both species were fed hay diets. Data from Foose (1982) confirms this pattern. Anatomical data compilations suggest that *E. maximus* has a longer gastrointestinal tract, a larger masseteric insertion area, and smaller parotid glands than *L.africana* (Clauss et al. 2007b) —seemingly in parallel to similar differences between GR and BR ruminants.

Hyraxes

The GR *Procavia capensis* and the more browsing *Heterohyrax brucei* and *Dendrohyrax dorsalis* have similar differences in microwear pattern as found in other herbivore taxons (Walker et al. 1978), but they have the same hypsodonty index (Janis 1990). No differences in tooth sharpness were observed between GR and BR hyraxes (Popowics and Fortelius 1997).

Suids

The suids comprise the GR warthog (*Phacochoerus aethipicus*) or the browsing/omnivorous babyrousa (*Babyrousa babyrussa*) and bushpig (*Potamochoerus porcus*), and the BR forest hog (*Hylochoerus meinertzhageni*; Harris and Cerling 2002; Mendoza et al. 2002; Cerling and Viehl 2004). Differences in hypsodonty (Harris and Cerling 2002; Mendoza et al. 2002) accord with observations in other taxonomic groups. Preliminary results indicate that *B. babyrussa* digests grass fibre less efficiently than domestic pigs (Leus and MacDonald 1997).

Ruminants

Results of uni- and bivariate analyses are given in Table 3.5. A multivariate analysis by Solounias and Dawson-Saunders (1988) using 13 traits mainly related to masseter muscle insertion in 27 species, and another multivariate analysis by Sponheimer et al. (1999) using four craniodental traits in 23 species, both found significant differences between the feeding types. In a multivariate, stepwise discriminant analysis of data from 72 bovid species, Mendoza and Palmqvist (2006a) demonstrated systematic differences in craniodental morphology between feeding types. With four exceptions, none of the studies listed in Table 3.5 were performed with phylogenetic control; therefore, although many characters do differ according to the predictions, it cannot be determined whether this represents a case of true convergent evolution. For physiological measurements such as digestibility (Robbins et al. 1995; Iason and Van Wieren 1999) or particle retention time (Gordon and Illius 1994; Hummel et al. 2006), larger datasets yielded different results than previous studies on more limited datasets. The fact that GR digest fibre more efficiently than BR (Pérez-Barbería et al. 2004) supports the general concept of feeding type differentiation. With respect to anatomical measurements of the forestomach, very few have been submitted to tests, and the basic dataset (Hofmann 1973) has hardly been expanded. In the multivariate analysis of Pérez-Barbería et al. (2001a), no specific functionality of the traits analysed was addressed; instead, the study tested whether Hofmann's conclusions could be supported or derived from the majority of the data given in Hofmann (1973). It was found that, after controlling for both body mass and phylogeny, the forestomach structures of BR and GR are similar, whereas those of mixed feeders differ; this finding is difficult to reconcile with the result that mixed feeders represent an intermediate evolutionary state between BR and GR (Pérez-Barbería et al. 2001b). Recently, it has been shown that GR have larger omasal laminal surface areas than BR (Clauss et al. 2006c), supporting Hofmann's (1968) observation that GR have larger omasa, and that BR have larger salivary glands (Hofmann et al., in press), confirming the indications of earlier studies. Even though the respective forages differ in fermentation rate (D2), it is difficult to predict in what way RR ingesta samples, which do not represent fresh forage but forage in varying states of fermentation (that is, proportions of which

Table 3.5 Statistical tests for morphological differences between grazing (GR) and browsing (BR) ruminants. FR = functional relevance, *n* = number of species, dg = data given (yes/no), od = original data (yes/no), FTC = feeding-type classification (d = discrete; c = continuous), FT = difference between grazers/browsers significant without/with phylogenetic control, BM = correlation with body mass significant without/with phylogenetic control. * = significant, ns = not significant, ds = difference in slope, - = not done

Parameter	FR	*n*	dg	od	FTC	FT	BM	Direction	Source
Braincase angle	A2	33	y	y	d	*/-		GR < BR	(Spencer 1995)
Glenoid height	A2	33	y	y	d	*/-		GR > BR	(Spencer 1995)
Paracondylar process	A2	33	y	y	d	*/-		GR > BR	(Spencer 1995)
Diastema length	A2, C3	33	y	y	d	*/-		GR > BR	(Spencer 1995)
Length of skull	A2, C3	33	y	y	d	*/-		GR > BR	(Spencer 1995)
Predental length	A2, C3	33	y	y	d	*/-		GR > BR	(Spencer 1995)
Incisor arcade breadth	A3	88	y	y	d	*/-	*/-	GR > BR	(Gordon and Illius 1988)
Incisor arcade breadth	A3	33	y	y	d	*/-		GR > BR	(Spencer 1995)
Incisor arcade breadth	A3	79	y	n	d	*/ns	*/*		(Pérez-Barbería and Gordon 2001)
Incisor arcade shape	A3	72	y	n	d	(ds)	ns/ns		(Pérez-Barbería and Gordon 2001)
Muzzle height (lip muscle attachment)	A3	27	y[a]	y	d	*/-		GR < BR	(Solounias and Dawson-Saunders 1988)
Parotid gland size	B4	22[b]	n	yn	d	*/-	*/-	GR < BR[c]	(Robbins et al. 1995)
Parotid gland size	B4	20	y	n	d	*/(-)		GR < BR	(Jiang and Takatsuki 1999)
Parotid gland size	B4	62	y	y	c	*/*	*/-	GR < BR	(Hofmann et al., in press)
Mandibular gland size	B4	61	y	y	c	*/*	*/-	GR < BR	(Hofmann et al., in press)
Size of the ventral buccal glands	B4	44	y	y	c	*/*	*/-	GR < BR	(Hofmann et al., in press)
Sublingual gland size	B4	30	y	y	c	*/*	*/-	GR < BR	(Hofmann et al., in press)
Hypsodonty index	C1-C2	27	y	n	c	*/-		GR > BR	(Sponheimer et al. 2003)
Hypsodonty index	C1-C2	37	y	n	c	*/-		GR > BR	(Cerling et al. 2003)
Hypsodonty index	C1-C2	13	n	n	c	*/-		GR > BR	(Codron et al. 2007b)
Molar wear rates	C1-C2	9	y	n	d	*/-	*/-	GR > BR	(Solounias et al. 1994)
Distance orbita tooth row	C1-C2	22	y	y	d	*/-		GR > BR	(Solounias et al. 1995)
Mandible depth	C1-C3	33	y	y	d	*/-		GR > BR	(Spencer 1995)
Mandible depth	C1-C3	27	n	n	c	*/-		GR > BR	(Sponheimer et al. 2003)
Mandible width	C1-C3	33	y	y	d	*/-		GR > BR	(Spencer 1995)

Tooth blade sharpness	C1-C2, C4	14	n	y	d	ns/-			(Popowics and Fortelius 1997)
Length of premolar tooth row	C3	33	y	y	d	*/-		GR < BR	(Spencer 1995)
Length of premolar tooth row	C3	27	n	n	c	*/-		GR < BR	(Sponheimer et al. 2003)
Masseter weight	C3	22	y	y	d	ns/-	*/-		(Axmacher and Hofmann 1988)
Masseter insertion area	C3	22	y	y	d	*/-		GR > BR	(Solounias et al. 1995)
Palatal width	C3	33	y	y	d	*/-		GR < BR	(Spencer 1995)
Molar cavity complexity	C4	27	y	y	d	*/-		GR > BR	(Solounias and Dawson-Saunders 1988)
Molar enamel ridge pattern/occlusal surface complexity	C4	26	y	y	d	*/-		GR > BR	(Archer and Sanson 2002)
Faecal particle size	C4, D2	81	y	y	d	*[d]/-	*/-	GR < BR	(Clauss et al. 2002)
RR capacity (water fill volume)	C4, C5, D2	25	n	n	d	*/-		GR > BR	(Demment and Longhurst 1987)
RR capacity (water fill volume)	C4, C5, D2	25	n	n	d	ns/-	*/-		(Van Wieren 1996b)
RR capacity (water fill volume)	C4, C5, D2	36	y	n	d	*/(-)		GR > BR	(Jiang and Takatsuki 1999)
RR contents (wet weight)	C4, C5, D2	21	y	n	d	ns[e]/-	*/-		(Gordon and Illius 1994)
RR contents (wet weight)	C4, C5, D2	21	y	n	d	*[f]/-	*/-	GR > BR	(Gordon and Illius 1994)
RR contents (wet weight)	C4, C5, D2	47	y	n	d	*/(-)		GR > BR	(Jiang and Takatsuki 1999)
RR contents (wet weight)	C4, C5, D2	29	y	n	d/c	*/-	*/-	GR > BR	(Clauss et al. 2003c)
RR contents (dry)	?	21	y	n	d	ns[e]/-	*/-		(Gordon and Illius 1994)
Rumen pillar thickness	C4, C5, D2	27	y	n	d/c	*/-	*/-	GR > BR	(Clauss et al. 2003c)
Rumen total surface area	C4, C5	45	y	y	d	*(ds)[g]/-		GR < BR	(Demment and Longhurst 1987)
Density papillation ventr. rumen	?	25	n	n	d	*[h]/-	*/-	GR < BR	(Van Wieren 1996b)
Maximum SEF (of any RR location)	?	25	n	n	d	ns/-	*/-		(Van Wieren 1996b)
Ostium rumino-reticulare[i]	?	25	n	n	d	-/-	*/-		(Demment and Longhurst 1987)
Omasal laminar surface area	C4, C5	34	y	y	c	*/*	*/*	GR > BR	(Clauss et al. 2006c)
RR liquid flow rate	D2	8	n[j]	yn	d	ns/-	*/-		(Robbins et al. 1995)
RR liquid retention time	D2	8	n	yn	d	?[k]			(Robbins et al. 1995)
RR liquid retention time	D2, C5	14	n	n	d	ns[l]/-	ns[l]/-		(Clauss et al. 2006c)
RR particle retention time	D2, C5	10	n	n	d	ns[m]/-	ns[m]/-		(Clauss et al. 2006c)

(continued)

Table 3.5 (continued)

Parameter	FR	*n*	dg	od	FTC	FT	BM	Direction	Source
RR VFA concentrations	B2, B3	16	y	y	d	*[n]/-	*/-	GR < BR	(Clemens and Maloiy 1983)
RR contents crude fibre content	B2	16	y	y	d	ns/-			(Woodall 1992)
RR fermentation rates (mols per DM and d)	B2, B3, D2	21	y	n	d	ns/-	*/-		(Gordon and Illius 1994)
Energy by VFA in RR per day	D2	21	y	n	d	*[o]/-	*/-	GR > BR	(Gordon and Illius 1994)
Energy by VFA in RR per day	D2	21	y	n	d	ns[p]/-	*/-		(Gordon and Illius 1994)
RR acetate:propionate ratio	B2-B3	16	y	y	d	ns/-	*/-		(Clemens et al. 1983)
Energy content of RR VFA (J per mol)	B2, B3[q]	21	y	n	d	ns/-	ns/-		(Gordon and Illius 1994)
RR acetate proportions	B2-B3	16	y	y	d	ns/-	ns/-		(Clemens et al. 1983)
RR propionate propotion	B2-B3	16	y	y	d	*/-	*/-	GR < BR	(Clemens et al. 1983)
RR butyrate proportion	B2-B3	16	n	y	d	ns/-	ns/-		(Clemens et al. 1983)
Dry matter RR (% of wet weight)	?	16	y	y	d	ns/-	ns/-		(Clemens and Maloiy 1983)
Volume omasum-abomasum	C4, C5	25	n	n	d	ns/-	*/-		(Van Wieren 1996b)
Ratio Vol. RR:Omas-Abomas	?	25	n	n	d	ns/-	ns/-		(Van Wieren 1996b)
DM abomasum (%)	C4, C5, D2	16	y	y	d	*/-	ns/-	GR > BR	(Clemens and Maloiy 1983)
DM small intestine (%)	C4, C5, D2	16	y	y	d	*/-	*/-	GR > BR	(Clemens and Maloiy 1983)
Hindgut contents (wet weight)	D2	15	y	n	d	*[r]/-	*/-	GR < BR	(Gordon and Illius 1994)
Caecum VFA concentration	B2, B3, D2	18	n	y	d	ns/-	-/-		(Maloiy and Clemens 1991)
Colonic VFA concentration	B2, B3, D2	16	y	y	d	*/-	ns/-	GR < BR	(Clemens and Maloiy 1983)
Hindgut VFA reabsorption	B2, B3, D2	16	y	y	d	*/-	ns/-	GR < BR	(Clemens and Maloiy 1984)
Hindgut fermentation rates	B2, B3, D2	15	y	n	d	ns/-	*/-		(Gordon and Illius 1994)
Energy by VFA in hindgut per day	D2	15	y	n	d	ns/-	*/-		(Gordon and Illius 1994)
Hindgut acetate:propionate ratio	B2, B3, D2	16	y	y	d	ns (*)[s]/-	ns/-	GR > BR	(Clemens et al. 1983)
Hindgut acetate proportions	B2, B3, D2	16	y	y	d	*/-	*/-	GR > BR	(Clemens et al. 1983)
Hindgut propionate propotion	B2, B3, D2	16	y	y	d	ns/-	ns/-		(Clemens et al. 1983)
Hindgut butyrate proportion	B2, B3, D2	16	n	y	d	*/-		GR < BR	(Clemens et al. 1983)
Lactic acid in caecum and colon	B2, B3, D2	16	y	y	d	*/-	*/-	GR < BR	(Clemens and Maloiy 1983)
Fiber digestion	D2	15	n	n	d	ns/-			(Robbins et al. 1995)

Fiber digestion	D2	20	n	n	d	*/-	ns/-	GR > BR	(Van Wieren 1996b)
Fiber digestion	D2	20	n	n	d	*/-	*[t]/-	GR > BR	(Iason and Van Wieren 1999)
Fibre digestion	D2	24	n	n	c	-/*	-/ns	GR > BR	(Pérez-Barbería et al. 2004)
Total GIT particle mean retention time	D2	26	y	n	d	ns[u]/-	*/-		(Gordon and Illius 1994)
Total GIT particle mean retention time	D2	33	n	n	d	*[u]/-	*/-	GR > BR	(Hummel et al. 2006)
Colonic fluid absorption	?	16	y	y	d	ns/-	ns/-		(Clemens and Maloiy 1984)
Dry matter distal colon (% of wet weight)	?	16	y	y	d	*/-		GR < BR	(Clemens and Maloiy 1983)
Dry matter faeces (% of wet weight)	?	81	y	y	d	ns[v]/-	*[w]/-		(Clauss et al. 2004)

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[a] data not measured but given as discrete categorical variables

[b] not all species stated in the methods can be found on the graph in the results

[c] the tragelaphinae, especially the greater kudu, were outliers to this pattern

[d] difference in slopes, GR < BR only in species >80 kg; only captive animals on zoo winter diets used

[e] see Clauss et al. (2003c); data compared to gut-content-free BM, using the authors' own feeding type classification

[f] using Hofmann's classification; not mentioned in results, only in discussion

[g] as observed (Pérez-Barbería et al. 2001a), the claim of statistical significance is not justified due to the difference in slopes

[h] significance disappeared when three small species were excluded; note that according tests (exclusion of certain species) were not performed in other analyses

[i] misquoted as the ostium reticulo-omasale (Illius and Gordon 1999; Gordon 2003); in contrast to the claim by these authors, no test for difference between feeding types is found in the original work

[j] not all data from the publications cited in methods section visible in the graph

[k] no evident pattern, unclear whether statistical test was performed, not all data from the publications cited in methods section visible in the graph

[l] number of species too small to allow confirmation or refutation of hypotheses; note that in pair-wise comparison, cattle had shorter RR fluid retention than large browsers

[m] number of species too small to allow confirmation or refutation of hypotheses

Table 3.5 (continued)

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[n] statistical significance could not be confirmed (Streich, pers. comm.)

[o] using their own feeding type classification; note that the individual factors used to calculate this factor (RR DM load, VFA production rate, VFA energy content) did not differ significantly

[p] using Hofmann's classification

[q] due to chemical composition of forages, no difference is to be expected

[r] using Hofmann's classification

[s] $p < 0.045$ is stated in the paper

[t] correlation with BM weak but significant

[u] see comments in text and in Clauss and Lechner-Doll (2001)

[v] wider ranges in faecal DM observed in GR than in BR

[w] decreasing faecal DM with BM

do not yield further volatile fatty acids), will reflect this. In particular, a large set of truly comparable ingesta passage measurements is missing.

3.6 Conclusion and Outlook

Although many of the morphophysiological adaptations expected in BR and GR (Table 3.2) seem to be met in tests using conventional statistical methods, the number of such characteristics tested with a phylogenetic control remains low to date (Tables 3.3-3.5). Most of the studies including phylogenetic controls have addressed ungulates as a phylogenetic group, whereas the according parameters have hardly been investigated within lower taxonomic units, such as the ruminants, or, also for lack of extant species, the hindgut-fermenting ungulates. In this respect, the findings of Pérez-Barberia et al. (2004), Clauss et al. (2006b), and Hackenberger (1987) on differences in digestive efficiency between feeding types in ruminants, rhinoceroses, and elephants should incite more comparative investigations in mechanisms involved in digestive physiology. Differences in the correlation between food intake and ingesta retention (Clauss et al. 2007c) could be particularly revealing for the differentiation of BR and GR. Controlled studies that measure retention time and digestibility, on both ad libitum intake of natural forages (which is hypothesised to result in different intake levels) and on similar intake levels of the same forages, could be performed in a multitude of species. Effects of forages should be tested by feeding the same amounts of different forages to a species. The variety of macropod, rodent (Kay and Madden 1997), suid and ruminant species offers an ideal research area for such future studies.

The craniodental patterns found in ruminants with conventional statistical methods should be evaluated within the ruminant guild by phylogenetically controlled studies. More experimental (engineering or biomechanical) approaches are warranted to corroborate the proposed adaptive relevance of craniodental parameters. Amongst others, the pioneering studies of Witzel and Preuschoft (1999, 2002, 2005) could serve as an example here. In order to test for potential differences in soft tissue morphology, new data on both macropods and ruminants is desperately needed, and until more cervid species are included in a phylogenetically controlled study, tests for convergent evolution within the ruminants must remain tentative. In terms of functional relevance, we think that soft tissue anatomy poses the most challenging questions that have to be addressed by engineering models, such as the one created by Langer and Takács (2004) addressing the functional relevance of taeniae and haustra in mammalian intestines, or by invasive experiments such as the one fashioned by Kaske and Midasch (1997) who impeded the motility of the reticulum in sheep in order to elucidate the role of this forestomach compartment for the digestive process in ruminants.

While a comparison of measurements of physiological processes, such as digestive efficiency, ingesta retention time, particle size reduction, amount of food ingested, etc., represent valuable bases for the discussion of different feeding types and their ecological impact on their feeding niches, we believe that only progress in the quantitative understanding of both the function of hard and soft tissue anatomical features and functionally relevant forage properties will allow meaningful interpretations of potential morphological adaptations. It is only by such knowledge that questions like whether different sets of adaptations, with an overexpression of one morphological feature compensating for the underexpression of another feature or vice versa, will facilitate the exploitation of the same niche; or whether the evolution of a particular anatomical feature exclusively allows the use of a new niche or broadens the range of niches available to the species, leaving open the path to a back-switching to formerly used niches. We want to conclude this chapter with the puzzling example of the ruminant reticulum, well aware that differences in this organ have not been statistically demonstrated between the feeding types. The reticular honeycomb cells of many grazing ruminants are particularly pronounced and deep (Hofmann 1988). In domestic ruminants, their function as sedimentation traps for small particles which are subsequently transported into the next forestomach compartment has been determined experimentally (Kaske and Midasch 1997). In contrast, many browsing ruminants, deemed representatives of evolutionary older ruminants, have extremely shallow reticular crests (Neuville and Derscheid 1929), the mechanical function of which is beyond imagination so far. Their shape could be explained if they could be considered 'atavisms', an interpretation ruled out by the common understanding of the evolutionary sequence of feeding types to date. Therefore, the shallow crests of roe deer, moose, and giraffe remain a challenging example for the fact that the evolution of morphological characters can only be understood by their functional relevance.

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Cover illustration: Zebras alerted by a predator in Mana Pools National Park in the Zambezi Valley, Zimbabwe. (Photo Iain J. Gordon)

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