FULL TITLE: Seasonal strategies differ between tropical and extratropical herbivores

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STATEMENT OF AUTHORSHIP

JOA conceived of the study. ACS and JOA designed analyses, with significant contribution from GPH. JOA compiled data, led analyses, and wrote the manuscript. GPH and JTF contributed to study design and manuscript development. All authors discussed ideas and provided manuscript feedback.

DATA ACCESSBILITY STATEMENT

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ABSTRACT

Seasonal diet shifts and migration are key components of large herbivore population dynamics, but we lack a systematic understanding of how these behaviors are distributed on a macroecological scale. The prevalence of seasonal strategies is likely related toherbivore body size and feeding guild, and may also be influenced by properties of the environment, such as soil nutrient availability and climate seasonality. We evaluated the distribution of seasonal dietary shifts and migration across large-bodied mammalian herbivores and determined how these behaviors related to diet, body size, and environment. We found that herbivore strategies were consistently correlated with their traits: seasonal diet shifts were most prevalent among mixed feeding herbivores and migration among grazers and larger herbivores. Seasonality also played a role, particularly for migration, which was more common at higher latitudes. Both dietary shifts and migration were more widespread among extratropical herbivores, which also exhibited more intermediate diets and body sizes. Our findings suggest that strong seasonality in extratropical systems imposes pressure on herbivores, necessitating widespread behavioral responses to navigate seasonal resource bottlenecks. It follows that tropical and extratropical herbivores may have divergent responses to global change, with intensifying herbivore pressure in extratropical systems contrasting with diminishing herbivore pressure in tropical systems.

INTRODUCTION

Herbivore population sizes determine the magnitude of their ecological impacts, their own conservation status, and their sensitivity to global change (Cardillo *et al.,* 2005; Estes *et al.,* 2011; Ripple *et al.,* 2015; Staver *et al.,* 2021). Two behaviors play an outsized role in allowing mammalian herbivores to achieve large populations by enabling them to circumvent seasonal resource bottlenecks (Illius & O'Connor, 2000): seasonal migration and seasonal dietary shifts (Staver & Hempson, 2020). In the case of migration, herbivores move to track seasonally fluctuating resources across the landscape (Aikens *et al.,* 2020; Fryxell & Sinclair, 1988). Large mammalian herbivore migrations, which are well-documented among tropical grazers, contribute to sustaining large populations in the face of seasonality (Fryxell & Sinclair, 1988; Staver & Hempson, 2020). In the case of dietary shifts, herbivores instead change their diets seasonally in response to local changes in resource quality and availability (Codron *et al.,* 2007; Kartzinel & Pringle, 2020). More limited evidence suggests that seasonal diet flexibility helps herbivores resist drought-induced mortality (Abraham *et al.,* 2019) and achieve large population sizes (Staver & Hempson, 2020), such that herbivores with seasonally variable diets often dominate savanna communities (Staver & Hempson, 2020). Though taxon- or system-specific case studies have explored the determinants of these strategies (see, *e.g.*, Abraham *et al.,* 2019; Aikens *et al.,* 2020; Fryxell & Sinclair, 1988; Gagnon & Chew, 2000), we lack evaluations of how these seasonal strategies are distributed globally.

There are several competing hypotheses that could explain the distribution of seasonal strategies, with varying degrees of taxon- and system-specific support. First, body size likely influences both herbivore metabolic requirements (Hopcraft *et al.,* 2010; Olff *et al.,* 2002) and the accessibility of seasonal strategies (Abraham *et al.,* 2019; Webber & McGuire, 2021). One possibility is that larger-bodied animals may be more able to vary their food sources seasonally, because they require food in large quantities rather than of high quality, and may consequently tolerate a broader range of diets (Bell, 1971; Hopcraft *et al.,* 2010; Jarman, 1974; Olff *et al.,* 2002). Larger herbivores might also be more migratory (Webber & McGuire, 2021), as they are less restricted in their landscape use by resource quality and predation (Hopcraft *et al.,* 2010; Veldhuis *et al.,* 2019) and are morphologically and energetically able to travel long distances (Bhat *et al.,* 2020; Hein *et al.,* 2012). An alternative possibility is that intermediate-bodied herbivores may instead diet switch more, as they are comparatively free from both the quality restrictions of their smaller-bodied counterparts and the quantity restrictions of large-bodied herbivores, affording them greater dietary flexibility (Hopcraft *et al.,* 2010; Veldhuis *et al.,* 2019). Intermediate-bodied taxa may also be the most migratory (*e.g.*, Jarman, 1974), as they are more gracile and cursorial (Hopcraft *et al.,* 2015; Scott, 1985). A final alternative is that seasonal diet shifts are most prevalent among small herbivores, because they require high quality vegetation all year long (Olff *et al.,* 2002), and so may switch to high-quality forage reservoirs as forage quality declines over the course of the growing season (Güsewell, 2004; Reich & Oleksyn, 2004; Scanlon *et al.,* 2005).

Body size could also predict the composition of herbivore diets as well as their seasonal strategies, resulting in covariation between diet composition and strategies. Metabolic scaling theory suggests that large herbivores may eat more grass, due to differences in how resource distributions and searching costs scale with body size (Bhat *et al.,* 2020). This pattern has been noted at a number of sites (*e.g.,* Arman & Prideaux, 2015; Bell, 1971; Gagnon & Chew, 2000; Jarman, 1974) but has not been evaluated globally. If true, grass intake might mediate the effects of body mass on seasonal strategies (Abraham *et al.,* 2019). Case studies from African savannas do indeed suggest that migration tends to be most common among specialist grazers (Abraham *et al.,* 2019; Fryxell & Sinclair, 1988; Jarman, 1974), whose resource base fluctuates predictably with rainfall seasonality (Scanlon *et al.,* 2005). Likewise, mixed feeders, which consume intermediate amounts of grass within a given season and are therefore depend in part upon seasonally fluctuating grasses (Codron *et al.,* 2007), seem uniquely able to shift their diets in response to declining grass biomass and nutrition (Abraham *et al.,* 2019), likely because mixed feeders have broader niches (Kartzinel & Pringle, 2020) and vegetation preferences that transcend plant functional types (Codron *et al.,* 2007).

A complementary perspective is that herbivore strategies depend on soil nutrient availability in interaction with rainfall, via effects both on herbivore traits and forage quality (Hempson *et al.,* 2015; Holdo *et al.,* 2009). Because large herbivores tolerate nutrient-poor vegetation (Olff *et al.,* 2002), they may dominate in environments with locally low and/or variable soil nutrient content (Hempson *et al.,* 2015; Hopcraft *et al.,* 2010) or high rainfall (Hempson *et al.*, 2015; Olff *et al.,* 2002). Similarly, because grass might be of higher quality in low rainfall, nutrient-rich habitats (Güsewell, 2004; Reich & Oleksyn, 2004; Scanlon *et al.,* 2005), grass-specialist herbivores might be more prevalent in such environments (Hempson *et al.,* 2015). As such, soil nutrient availability and rainfall together might impact the spatial distributions of herbivore traits, with implications for the distributions of herbivore strategies. Indeed, interactions between soil nutrients and rainfall have been implicated in driving migration: some herbivore migrations track opposing rainfall and soil nutrient gradients (Holdo *et al.,* 2009). Diet-switching may similarly be more beneficial in nutrient-rich environments (Abraham *et al.,* 2019; Staver & Hempson, 2020), as plant quality may be more variable (both between plants and across seasons) (Güsewell, 2004; Reich & Oleksyn, 2004).

A final possibility is that seasonality shapes herbivore strategies. Because these behaviors are responses to seasonal resource bottlenecks (Illius & O'Connor, 2000; Staver & Hempson, 2020), the strength of seasonality might determine the prevalence of strategies. In the tropics and subtropics, pronounced rainfall seasonality drives predictable changes in grass biomass and nutrition but more varied seasonal changes in the tree layer (Ryan *et al.,* 2017; Scanlon *et al.,* 2005), altogether translating into differential seasonal resource availability across plant functional types. Higher latitudes are characterized instead by strong temperature and sometimes also moisture seasonality, resulting in dramatic temporal variability in productivity and biomass across most plants (Running *et al.,* 2004; Xu *et al.,* 2013) (see Fig 1). Thus, whereas scarcity-mitigating behaviors might be restricted to a subset of herbivores in tropical regions (particularly grass-dependent taxa; Abraham *et al.,* 2019; Fryxell & Sinclair, 1988; Jarman, 1974), strategies for mitigating scarcity might be more widespread at higher latitudes (Aikens *et al.,* 2020; Albon & Langvatn, 1992; Bolger *et al.,* 2007; Singh *et al.,* 2012). Indeed, some evidence (primarily from high latitude cervids) indicates that at least migration may be more widespread across species in more seasonal environments (Aikens *et al.*, 2020; Singh *et al.*, 2012), though large-scale demonstrations of this pattern are also lacking.

Overall, we hypothesize (1) that herbivore body size and grass consumption play key roles in determining herbivore seasonal strategies, but (2) that environmental characteristics, particularly soil nutrient availability and the magnitude of seasonality, also influence the distribution of these strategies among large-bodied mammalian herbivores. While these hypotheses are longstanding, with varying degrees of site- or taxon-specific support, comprehensive empirical evaluations of these patterns at macroecological scales are lacking. To address this gap, here we synthesize herbivore traits and behaviors to evaluate the distribution of seasonal strategies among large mammalian herbivores globally, employing model selection to identify the best predictors of herbivore traits and strategies.

METHODS AND MATERIALS

Defining large mammalian herbivores

First, we generated a comprehensive list of large-bodied herbivorous mammals using the EltonTraits 1.0 database, a global species-level compilation of 5,400 mammal species' foraging traits (Wilman *et al.,* 2014). Data include mean adult body masses, as well as dependences on broad food categories (*e.g.,* invertebrates, vertebrate ectotherms, vertebrate endotherms, fruit, seeds, leaves/other plant tissue, etc.). We filtered the database for mammals ≥ 5 kg (Kartzinel & Pringle, 2020) and with diets of ≥ 70% leaf material to exclude carnivores and omnivores. We excluded herbivores that are extinct in the wild and herbivores categorized as arboreal, aquatic, or flighted, as these modes of locomotion result in distinct physiological constraints, such that generalizing across locomotor modes is not appropriate (Hein *et al.,* 2012). This resulted in a list of 238 large-bodied herbivorous mammal species, including most terrestrial Artiodactyla, several species from the orders Diprotodontia, Perissodactyla, Rodentia, Proboscidea, and Primates, and one Carnivora species.

Quantifying environmental drivers

To compile data on the seasonality experienced by each herbivore species, we downloaded expert geographic range maps from IUCN (2019). We averaged mean annual precipitation, mean rainfall seasonality (Fig. 1b), mean annual temperature, and mean temperature seasonality (Fig. 1c) across each herbivore's range using climatic data from

WorldClim 2.0 at a spatial resolution of 30 minutes (Fick & Hijmans, 2017). For all these variables, we also calculated the standard deviation across an herbivore's species range (Fig. 1b,c) to capture spatial variation in each predictor.

Seasonality varied substantially across the terrestrial landmass (Running *et al.,* 2004), with pronounced rainfall seasonality but low temperature seasonality in the tropics and subtropics and lower rainfall seasonality but consistent temperature seasonality in the extratropics (temperate, boreal, and polar regions) (Fig. 1). We therefore classified herbivores as either 'tropical' or 'extratropical'. We calculated the centroid of species ranges from WGS84 ellipsoid areas of IUCN species range maps, excluding the introduced portions of ranges (Fig. 1a); herbivores were categorized as 'tropical' if their range centroids were < 35˚ N/S or 'extratropical' if their range centroids were > 35˚ N/S. We chose 35˚ N/S (the limit of the subtropics) as the boundary because, during winter, regions outside of 35˚ N/S frequently experience subzero temperatures and the regular formation of a sustained snowpack, such that the severity of seasonal resource bottlenecks differs substantially across this threshold (plants not only stop growing, but also become physically inaccessible; Running *et al.*, 2004; Xu *et al.*, 2013). However, to evaluate the sensitivity of our results to this classification criterion, we also ran all comparisons between tropical and extratropical herbivores using 23.5˚ N/S (Tropics of Cancer/Capricorn) as the boundary (see *Data analyses*). Note that results did not differ qualitatively between these two different classification criteria (Table S8).

Direct evaluations of the role of forage quality in driving herbivore seasonal strategies were not possible here, as global datasets of plant nutrient content are lacking. However, plant nutrient content is influenced by both local soil nutrients and rainfall (Güsewell, 2004; Reich & Oleksyn, 2004; Scanlon *et al.*, 2005). Therefore, for insight into whether forage quality may play a role in influencing the distribution of seasonal strategies, we compiled soil nutrient data from World Soil Information Service (WoSIS) (Batjes *et al.,* 2017). We used the raw data underlying the WoSIS global soil data layer. We took all points that were above 60 cm depth, corresponding to plant-available nutrients (Güsewell, 2004; Reich & Oleksyn, 2004), within each species' range. We calculated the mean, standard deviation, and range for both effective cation exchange capacity (CEC) and soil nitrogen content. For some herbivores (51 species), no soil data were available, and these taxa were excluded from analyses involving soil nutrients (see *Data analysis*).

Herbivore body mass and diet traits

Next, we compiled data on herbivore body mass and diet. Herbivore body mass data were available from EltonTraits 1.0 (Wilman *et al.,* 2014), which are themselves compilations from primary literature. Because herbivore body masses span multiple orders of magnitude (5 kg – 4,000 kg), body mass values were log-transformed for all analyses.

One of our major hypotheses was that herbivore grass dependence might explain the distribution of seasonality-mitigating behaviors, particularly in the tropics (Abraham *et al.,* 2019; Fryxell & Sinclair, 1988). We therefore performed a targeted literature search to determine the seasonal grass dependence – defined here as dietary grass fraction averaged over a given season – for each herbivore. Though there can be substantial diet variability between herbivore populations (Codron *et al.,* 2007), the use of representative dietary studies can provide a general and comparable metric for herbivore diets at the level of plant functional type (Gagnon & Chew, 2000). Thus, using Web of Science and Google Scholar, we found published studies that reported seasonal herbivore diet composition at the functional level (grass vs. browse) or at finer taxonomic scales. We recorded herbivore diet composition in both the growing season (summer/wet season) and dormant season (winter/dry season), as reported in the same study. Our search terms were 'diet' or 'diet composition' coupled with an herbivore's scientific name and/or common name. We included only those studies where percentages of different plant types were reported in both seasons, as determined by analysis of either herbivore gut contents or feces composition. These seasonal diet data were then used to calculate seasonal diet shifts. Dietary shifts were defined as the absolute value of the change in dietary grass fraction from the growing to the dormant season ($|\Delta \text{ diet}_{\text{grow-dorm}}|$) and therefore take positive proportional values (0-1). Herbivores without such published information (28 species) were excluded.

This methodology resulted in a list of 210 herbivorous mammals in 7 orders and 23 families distributed across the globe (Fig. 1) (see Supporting Information for a complete list of herbivores included in this study and all associated data and references).

Evaluating herbivore migration

To determine the distribution of migration across herbivores, we first compiled published syntheses cataloguing migratory animals (*e.g.,* Berger, 2004; Bergesen *et al.,* 2018; Bolger *et al.,* 2007; Harris *et al.,* 2009). For species not included in the aforementioned syntheses, we performed a literature search using Web of Science and Google Scholar to find records of migration, as we did above for herbivore diet composition. We searched each herbivore's scientific name and/or common name along with the search terms 'migrate', 'migratory', and/or 'migration' (see Supporting Material for references).

We reduced migration to a binary: herbivores were considered migratory (1) if there were any records of them having ever exhibited migratory behavior of any sort, past or present, or non-migratory (0) if there were not. We therefore coded species as migratory (1) if they were shown to undergo seasonal, round-trip movements between discrete areas (Berger, 2004; Bolger *et al.,* 2007) and/or if they were explicitly described as migratory in published literature (including if they exhibited elevational migration). Herbivores were recorded as non-migratory (0) if it was stated explicitly that they never migrate and/or if no published records of migratory behavior were available. We did not restrict our definition to mass migrations, where individuals of a species migrate *en masse*, as has been the case in previous cross-species syntheses (*e.g*., Harris *et al.,* 2009). This inclusive approach enabled us to capture any history of migration and to control against the confounding influence of anthropogenic restrictions on migratory behavior (Berger, 2004; Bolger *et al.,* 2007).

Data analysis

Data were analyzed in R 3.6.1 (R Core Team, 2020). We modeled traits and strategies using generalized least squares regression with a phylogenetic variance-covariance matrix (PGLS) via the *nlme*::*gls* function (Pinheiro *et al.,* 2007) to account for the phylogenetic non-independence of taxa (Paradis *et al.,* 2004). Indeed, the accessibility of these strategies is thought to be phylogenetically constrained (Fig. S1); rhinos and macropodids (kangaroos and relatives), for example, conspicuously lack migratory behavior (Kaufmann, 1974; Walker *et al.,* 1968). We therefore used a mammal-wide phylogeny constructed by Upham *et al.* (2019) pruned to the 210 herbivores included in our dataset (Fig. S1). Phylogenetic variance-covariance matrices were calculated from the pruned herbivore-only tree using *ape::corMartins* (Paradis *et al.,* 2004).

First, we built global models of body mass, grass dependence, migration, dietary shifts, and herbivore species range size that included all plausible predictors (see Tables S2-3). We employed a binomial distribution for our global model of migration, as it was coded as a binary, and Gaussian distributions for all other global models. Then, to determine which predictors best explained each of these variables, we built models including all permutations of explanatory variables and compared model-corrected Akaike Information Criterion (AIC_c) to assess model fit (Tables S4-7). We consider all models with $\Delta AIC_c < 2$ as 'preferred' models and have selected the simplest model within $\Delta AIC_c < 2$ as the overall 'best' model for the purposes of interpretation. We confirmed that all 'preferred' models satisfied modeling assumptions by inspecting model diagnostic plots.

We performed this model selection approach on five different data subsets (Tables S3-6): (a) all herbivores for which soil nutrient data were available ($N = 159$), (b) all herbivores ($N = 210$) but excluding all soil nutrient variables from global models, (c) only herbivores less than 500 kg ($N = 192$), (d) only herbivores between 50 kg and 500 kg ($N = 81$), and (e) only ungulates (herbivores in the orders Artiodactyla and Perissodactyla; $N = 175$). Results are consistent across all five datasets unless otherwise noted.

Next, we performed a phylogenetic paired *t*-test with the *phytools::phyl.pairedttest* function (Garland *et al.*, 1993; Lindenfors *et al.*, 2010; Revell, 2012) to compare the grass dependence of herbivores between the growing season and dormant season to determine how the functional composition of herbivore diets changes across seasons. We repeated this test using only the subset of herbivores that exhibit any amount of seasonal diet shift ($|\Delta\ \text{diet}_{\text{grow-dorm}}| > 0$; $N = 143$) to evaluate the magnitude of dietary shifts for those herbivores that exhibit any seasonal diet variation at all.

We then performed phylogenetic analyses of variance (phylANOVA) to explicitly compare traits and strategies between tropical and extratropical herbivores using *phytools::phylANOVA* (Garland *et al.*, 1993; Lindenfors *et al.*, 2010; Revell, 2012). We performed separate tests to evaluate if extratropical and tropical herbivores differed in their mean body mass, mean dependence on grass, propensity for migration, and magnitude of seasonal diet shifts. Likewise, we performed Kolmogorov–Smirnov tests (KS tests) to compare whether the distributions of these traits and strategies differed between extratropical and tropical herbivores using *stats::ks.test*. We did this for all five data subsets from above, and also using both 35° N/S and 23.5° N/S as the boundary separating tropical and extratropical herbivores (Table S8). Because results were largely the same regardless of which classification criteria was used, we present only the results with 35° N/S as the boundary in *Results* (but see Supporting Material for both sets of results). Also, as above, we subsetted our dataset for only herbivores that exhibit some amount of seasonal dietary shifting (*i.e.,* with $|\Delta \text{ diet}_{\text{grow-dorm}}| > 0$; $N = 143$) to specifically test if extratropical and tropical herbivores differed in the magnitude of seasonal diet shifts, again using *phylANOVA*.

When 35° N/S was used as the boundary between tropical and extratropical herbivores, tropical herbivores vastly outnumbered extratropical herbivores ($N_{trop} = 164$, $N_{extr} = 46$). Therefore, to account for these differences in sample size, we used bootstrapping: we randomly subsampled our dataset for *ca.* 30% of tropical herbivores ($N = 30$-66) and all extratropical herbivores ($N = 46$) and reran analyses on this subset 1,000 times. Here we report 95% confidence intervals on observed relationships across bootstrap iterations and/or the number of bootstrap iterations for which relationships were significant ($P < 0.05$). This was not necessary when 23.5° N/S was used as the boundary, as the numbers of herbivores in each group were more balanced ($N_{trop} = 118$, $N_{extr} = 92$).

RESULTS

Herbivore traits and strategies

Herbivore body mass was not predictable from any of the environmental variables included here (Table S4). The intercept-only model was the preferred model. Temperature variables (both mean annual temperature and spatial variation in mean annual temperature) were included in lower ranked models, as were soil nutrient variables. However, these models were not preferable to the null model, indicating that temperature and possibly also soil nutrient content may contribute to determining herbivore body size but seem to play only a minor role at macroecological scales.

Grass consumption was best predicted by herbivore body mass alone (Table S5). For all data subsets excepting herbivores between 50 kg and 500 kg, the best model of grass dependence included body mass as the sole predictor (Table S5). In all cases, body mass had a positive effect on herbivore grass consumption (Fig. 2), indicating that larger-bodied species were more grass dependent. For herbivores between 50 kg and 500 kg, the best model was the intercept only model, though the model with body mass as the sole predictor of grass dependence remained a preferred model (Table S5). This suggested that the relationship between grass dependence and body mass largely resulted from the smallest and largest herbivores, and that herbivores in this intermediate body size envelope were comparatively unconstrained in their diets (Fig.2. Results were consistent whether average, growing season, or dormant season grass consumption data were used.

Migration was best predicted by latitude, growing season grass dependence, and body mass. All three variables had a positive effect on migration (Fig. 3), with larger grazers at high latitudes most likely to migrate. The predictive power of body mass diminished when only herbivores between 50 and 500 kg were considered, replaced instead by spatial variation in mean annual temperature (Table S6). We found some support for both non-linear and linear relationships between migration and body mass, though a non-linear relationship only marginally improved model fit (Table S6). Also, when herbivores > 500 kg were excluded, a linear relationship was preferred to a non-linear one (Table S6). As such, we interpret our analyses to suggest that migration is indeed most widespread among larger-bodied taxa, rather than among herbivores of intermediate size. We found that no herbivores < 20 kg were migratory (Fig. 3a), possibly suggesting a morphological or energetic lower bound below which migration is infeasible (Brown *et al.,* 2004; Hein *et al.,* 2012; Joly *et al.,* 2019; Kaufmann, 1974).

Seasonal diet shifts were best predicted by an herbivore's growing season grass dependence alone (Table S7) across all data subsets, with diet shifts that peaked at intermediate grass dependencies (Fig. 4); herbivores with mixed diets even in the growing season (*e.g.,* herbivores that consumed both grass and browse even when resources were abundant) exhibited the largest seasonal diet shifts, whereas herbivores that were specialized on either grass or browse in the growing season exhibited smaller seasonal shifts in their diets.

Across all herbivores, diets typically shifted to incorporate more grass during the growing season (Fig. S1). Herbivores consumed on average 4.6% [2.7%, 6.5%] more grass during the growing season than during the dormant season (phylogenetic paired *t*-test; $df = 207$, $t = 4.801$, $P < 0.001$), indicating a preference for grass when it is growing and comparatively nutrient-rich (Scanlon *et al.,* 2005). Among herbivores that exhibited any seasonal diet variation (*i.e.,* with $|\Delta\text{diet}_{\text{grow-dorm}}| > 0$), dietary grass content increased by 6.9% [4.2%, 9.6%] in the growing season relative to the dormant season (phylogenetic paired *t*-test; $df = 140$, $t = 5.038$, $P < 0.001$). Thus, while mean increases in growing season grass consumption were 4.6% across all herbivores, an increase of 6.9% more accurately reflects the expected diet shift for an herbivore that exhibited any seasonal diet variation. Still, seasonal diet shifts were much larger than this for some herbivores: predicted seasonal diet shifts peaked at *ca.* 20% for herbivores with intermediate diets (mixed feeders) (Fig. 4).

Tropical and extratropical herbivores

Extratropical and tropical herbivores did not differ in their mean body masses (phylANOVA; *df* = 208, *F* = 0.824, *P* = 0.591), but the distributions of body masses differed significantly (KS test; *D* = 0.262, *P* = 0.011), with comparatively fewer extratropical herbivores at the extremes of the body size continuum (Fig. S2). Extratropical and tropical herbivores also had similar grass dependencies, both in mean (phylANOVA; *df* = 208, *F* = 0.444, *P* = 0.712) and in distribution (KS tests; *D* = 0.184, *P* = 0.176). For both extratropical and tropical herbivores, diet distributions were roughly trimodal, with the largest peak corresponding to 0-20% dietary grass (browsers), the next largest peak 80-100% grass (grazers), and the final peak at 40-60% grass (mixed feeders) (Fig. S2). These three peaks were particularly evident during the dormant season (Fig. S2).

In contrast, the role of body size in determining herbivore grass dependence differed between tropical and extratropical herbivores. The relationship between grass dependence and body mass disappeared when only extratropical herbivores were considered (PGLS; *df* = 44, *t* = 0.696, *P* = 0.490), but was robust when only tropical herbivores were considered (PGLS; *df* =162, *t* = 3.541, *P* < 0.001). Differences between tropical and extratropical herbivores were not an artefact of different sample sizes; when we bootstrapped tropical herbivores to extratropical sample sizes (×1,000 iterations), grass dependence consistently increased with body size (slope = 0.1663; 95% CI = [0.021, 0.311]).

Migration was more widespread among extratropical herbivores than tropical herbivores (phylANOVA; *df* = 207, *F* = 33.537, *P* = 0.001). This result held regardless of whether only ungulates were considered (phylANOVA; *df* = 172, *F* = 37.108, *P* = 0.001), only herbivores smaller than 500 kg (phylANOVA; *df* = 189, *F* = 36.796, *P* = 0.001), or only herbivores between 50 kg and 500 kg (phylANOVA; *df* = 78, *F* = 11.609, *P* = 0.007), and was significant in 999 of 1,000 bootstrap iterations. Likewise, the distribution of migration differed substantially between extratropical and tropical herbivores (KS test; D = 0.444, *P* < 0.001), being more widespread across body sizes and feeding guilds among extratropical herbivores (Fig. S2). Indeed, migration was nearly ubiquitous among extratropical herbivores > 20 kg (Fig. 3).

Finally, extratropical and tropical herbivores differed somewhat in their dietary flexibility (phylANOVA; *df* = 207, *F* = 10.115, *P* = 0.013). Extratropical herbivores exhibited larger diet shifts than did tropical herbivores, altering their diets on average 1.2% [1.0%, 1.4%] more between seasons than tropical herbivores. When only herbivores that exhibited some amount of seasonal diet shifts (*i.e.,* with $|\Delta \text{ diet}_{\text{grow-dorm}}| > 0$) were considered, however, tropical and extratropical herbivores did not differ in the magnitude of these seasonal diet shifts (phylANOVA; *df* =140, *F* = 1.977, *P* = 0.434). Taken together, these results suggest that the difference between extratropical and tropical herbivores is in the proportion of herbivores that shift their diets rather than the magnitude of the dietary shifts (Table 1). The distribution of diet shifts differed somewhat between extratropical and tropical herbivores (KS test; *D* = 0.364, *P* = 0.001), though this result is likely a sample size artifact, as diet shifts were more prevalent among extratropical herbivores in only 505 out of 1,000 bootstrap iterations of the tropical herbivore subsets.

DISCUSSION

Altogether, our results resolve long-standing uncertainties regarding what constrains herbivore strategies and demonstrate that several key hypotheses, hitherto only suggested from metabolic theory and scattered case studies, scale up to explain covariation in herbivore body size, diet, and seasonal strategies at macroecological scales. In particular, we found (1) that grass consumption increased with body size across large-bodied mammalian herbivores, but that this relationship broke down among extratropical herbivores. Also, (2) migration was more prevalent among grass-dependent herbivores, at high latitudes, and among large-bodied herbivores. In contrast, (3) herbivores with intermediate growing season grass dependency (*i.e.*, mixed feeders) exhibited the largest seasonal diet shifts. Finally, (4) though extratropical herbivores were more restricted in body size and grass dependency, they more ubiquitously employed seasonal strategies.

First and foremost, we found support for the hypothesis that body size and grass dependence influenced seasonal strategies (see also Abraham *et al.,* 2019). As predicted, migration was most common among relatively large species (Webber & McGuire, 2021), perhaps because, as modeling work suggests (Bhat *et al.,* 2020; Hein *et al.,* 2012), their energetic costs of movement are lower. We found that no herbivores below 20 kg were migratory, implying a lower bound for body size below which migration is not energetically or morphologically feasible (Hein *et al.,* 2012; Scott, 1985). Indeed, such a lower bound on migration has been invoked to explain the conspicuous lack of migration among extant kangaroos and their relatives (Kaufmann, 1974; McGowan *et al.,* 2008), which straddle this body size threshold (McGowan *et al.,* 2008).

Interestingly, body size did not appear to influence the distribution of seasonal diet shifts, except insofar as it determined grass dependence. Larger-bodied species consumed more grass (Bell, 1971; Janis, 2008; Jarman, 1974): because grass is a homogeneous and widespread forage pool relative to other plant functional types (Bhat *et al.,* 2020; Toljagić *et al.,* 2018), specializing on grass may allow large herbivores to minimize searching costs associated with their bulky forage requirements (Bhat *et al.,* 2020; Hopcraft *et al.,* 2010) (though the mechanism underpinning this relationship is not entirely resolved; Table 1). Though grass seemingly better fits the energetic needs of large herbivores as compared to small herbivores (Bhat *et al.,* 2020), body size explained only *ca.* 9% of the variation in grass dependence across herbivores, suggesting that other factors not captured in our analyses contribute to determining herbivore grass dependence (Table 1).

Grass dependence in turn plays a key role in promoting herbivore strategies, more even than body size. Migration was most prevalent among grass-dependent herbivores, a relationship that has long been noted across African savannas (Fryxell & Sinclair, 1988; Jarman, 1974), but appears to hold more globally. Indeed, grass productivity is comparatively responsive to seasonality relative to other plant functional types (Scanlon *et al.,* 2005), such that grass-specialist herbivores seem to employ migration to navigate seasonal changes in grass availability and quality (Fryxell & Sinclair, 1988). Relatedly, seasonal diet shifts were most prevalent among mixed feeders, defined as herbivores that consume intermediate amounts of grass even during periods of abundance. Mixed feeders have broad dietary niches that transcend plant functional types (Kartzinel & Pringle, 2020), and our results suggest that a wide dietary niche may be crucial for allowing seasonal dietary flexibility. As such, some axis of herbivore biology clearly influences the plants that herbivores utilize (Abraham *et al.,* 2019; Kartzinel & Pringle, 2020), though it is unclear if dietary niche breadth is determined by physiology/morphology (specific adaptations to diet; Toljagić *et al.,* 2018) or behavior (distinct preferences for vegetation types; Gagnon & Chew, 2000) (Table 1).

Our finding that body size and grass dependence are interconnected and mediate herbivore strategies, particularly migration, has intriguing implications for herbivore evolution (Table 1). Other work has posited that large body sizes in mammalian herbivores may have evolved with the proliferation of grasses as a result of a more homogeneous resource-scape (Bhat *et al.,* 2020; Janis, 1993, 2008), and the global relationship between body size and grass dependence we recover lends credence to this possibility. Still, large-bodied herbivores exist in the fossil record well before the proliferation of grasses (Janis, 1993; Smith *et al.,* 2010). As such, the relationship between body size and grass consumption may be an exaptation; mammals may have already been large for other reasons, but then evolved to specialize on grasses with their rise to dominance due to the unique nutrient profile and spatial distribution of grasses (Bhat *et al.,* 2020; Janis, 2008; Scanlon *et al.,* 2005). Relatedly, migration may play a role in moderating the relationship between grass consumption and body size: large herbivores may have been uniquely able to migrate and could thereby track grass productivity across the landscape, resultantly becoming increasingly specialized on grass (Bhat *et al.,* 2020; Fryxell & Sinclair, 1988; Toljagić *et al.,* 2018). Though we find strong evidence that these three phenotypes – migration, large body size, and grass dependence – are linked, the causality of these relationships remains unclear. Further studies should explicitly investigate the directionality of these relationships via the fossil record and/or phylogenetic analyses.

Our results suggest that soil nutrient levels do not play a large role in determining herbivore traits or strategies, contradicting hypotheses from metabolic theory (Olff *et al.,* 2002) and evidence from African ecosystems that bulk-feeders dominate in high rainfall (nutrient-poor) environments (Hempson *et al.,* 2015). On the one hand, differences in forage quality between plant functional types may decouple herbivores from soil nutrition (Güsewell, 2004; Reich & Oleksyn, 2004). Alternatively, soils data may simply be inadequate. As such, regional studies may be necessary to determine the role of soil nutrients in constraining herbivore traits and strategies (see, *e.g*., Hempson *et al.,* 2015).

Finally, we found that seasonality did influence herbivore body size and grass dependence and also increased the incidence of seasonal strategies, in line with existing hypotheses (Aikens *et al.,* 2020; Albon & Langvatn, 1992; Bolger *et al.,* 2007; Singh *et al.,* 2012). Seasonal strategies were more widespread among extratropical herbivores (Fig. 5), especially migration, which was far likelier at higher latitudes. Seasonal forage bottlenecks may be stricter at higher latitudes (as plants not only stop growing during the dormant season but can also become physically inaccessible under ice/snow; Albon & Langvatn, 1992; Bolger *et al.,* 2007; Singh *et al.,* 2012), or temperature seasonality may simply impose seasonally harsh climatic conditions (Shaw, 2016).

Latitudinal effects on body size and diet were more complex. Extratropical herbivores tended to have intermediate phenotypes (Fig. 5); although they did not differ in average body size or grass dependence from tropical herbivores, extratropical herbivores occupied a smaller range of body sizes and grass dependences. They were neither especially large nor small (see also Freckleton *et al.,* 2003) and consistently incorporated more mixed diets. Additionally, the clear increase in grass dependence with body size observed across all and tropical herbivores broke down among extratropical herbivores (Fig. 2c), perhaps because large, grass-dependent herbivores are missing from the herbivore community. These results together suggest that extratropical herbivores may be less able to specialize on any one plant functional type. It may also be the legacy of the size-selective extinction of Pleistocene megafauna (Barnosky, 2004), which was particularly severe among large-bodied grazers (Schowanek *et al.*, 2021).

Our results have multiple implications for herbivore ecology in a changing world. Firstly, extratropical herbivores may be comparatively well-equipped to respond to global change: as high latitude regions warm and seasonality in productivity potentially decreases (Xu *et al.,* 2013), extratropical herbivores may experience some relief from the intense competition that characterizes extratropical winters (Illius & O'Connor, 2000). Indeed, ballooning ungulate populations in many extratropical ecosystems around the world suggest that this may already be the case (Cote *et al.,* 2017; although this pattern is certainly due in part to the extirpation of natural predators, see Estes *et al.,* 2011). By contrast, tropical herbivores are experiencing increasing pressure from poaching, direct land-use change, and fragmentation of remaining wildland, in tandem with climate-driven physiological stress (Veldhuis *et al.,* 2019) and decreases in productivity (Cardillo *et al.,* 2005). Here we find that comparatively fewer tropical herbivores possess strategies for coping with variable resource availability (see also (Abraham *et al.,* 2019), which puts tropical herbivores lacking such strategies at risk of decline. Widespread population declines that have already been documented among tropical herbivores (Ripple *et al.,* 2015) are therefore likely to continue, with cascading effects on vegetation as plants are freed from widespread herbivory pressure (Estes *et al.,* 2011; Staver *et al.,* 2021). All in all, these results suggest diverging trajectories for tropical and extratropical herbivores in the face of global change.

CONCLUSIONS

We provided the first global-scale test of longstanding hypotheses about factors influencing body mass, diet, and seasonal strategies across medium to large mammalian herbivores. We found that larger hebrivores tended to eat more grass, and that seasonal diet shifts and migration were influenced by body mass and grass dependency, as well as the seasonality of their environments. Indeed, we found that these seasonal behaviors were altogether more widespread among extratropical herbivores, despite their intermediate diets and body sizes. Together, these results imply that extreme seasonality in extratropical systems imposes severe pressures on herbivores therein. As a result of extreme resource variability, extratropical herbivores occupy a more restricted phenotypic space, exhibiting more intermediate body sizes and generalist diets, while simultaneously exhibiting more widespread behavioral strategies for mitigating these seasonal bottlenecks (Fig. 5).

Our findings confirm hypotheses from scattered case studies and suggest many avenues for future research (see Table 1 for a set of possibilities), with far-reaching conservation implications. Most directly, these results indicate that extratropical herbivores may be well-suited to navigating global change. Extratropical herbivores may be able to utilize existing strategies to respond to changing productivity patterns (Xu *et al.,* 2013), which could increase top-down regulation of plant communities in extratropical regions (Cote *et al.,* 2017). By contrast, in the tropics, where the distribution of these behaviors is more restricted, herbivores may be less able to respond to changing resource distributions (Abraham *et al.,* 2019; Cardillo *et al.,* 2005; Ripple *et al.,* 2015). These results add to a growing body of literature emphasizing the precarious position of large-bodied tropical herbivores in a human-dominated future (Abraham *et al.,* 2019; Cardillo *et al.,* 2005; Estes *et al.,* 2011; Ripple *et al.,* 2015; Staver *et al.,* 2021).

Conservation efforts will therefore necessarily differ between extratropical and tropical systems and must strike a difficult balance between mitigating increased herbivore impacts in extratropical systems while protecting large-bodied herbivores in the tropics.

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REFERENCES

Abraham, J. O., Hempson, G. P., & Staver, A. C. (2019). Drought-response strategies of savanna herbivores. *Ecology and Evolution*, *9*(12), 7047–7056. https://doi.org/10.1002/ece3.5270

Aikens, E. O., Mysterud, A., Merkle, J. A., Cagnacci, F., Rivrud, I. M., Hebblewhite, M., Hurley, M. A., Peters, W., Bergen, S., De Groeve, J., Dwinnell, S. P. H., Gehr, B., Heurich, M., Hewison, A. J. M., Jarnemo, A., Kjellander, P., Kröschel, M., Licoppe, A., Linnell, J. D. C., … Kauffman, M. J. (2020). Wave-like Patterns of Plant Phenology Determine Ungulate Movement Tactics. *Current Biology*, *30*(17), 3444-3449.e4. https://doi.org/10.1016/j.cub.2020.06.032

Albon, S. D., & Langvatn, R. (1992). Plant Phenology and the Benefits of Migration in a Temperate Ungulate. *Oikos*, *65*(3), 502–513. https://doi.org/10.2307/3545568

Arman, S. D., & Prideaux, G. J. (2015). Dietary classification of extant kangaroos and their relatives (Marsupialia: Macropodoidea). *Austral Ecology*, *40*(8), 909–922. https://doi.org/10.1111/aec.12273

Barnosky, A. D. (2004). Assessing the Causes of Late Pleistocene Extinctions on the Continents. *Science*, *306*(5693), 70–75. https://doi.org/10.1126/science.1101476

Batjes, N. H., Ribeiro, E., van Oostrum, A., Leenaars, J., Hengl, T., & Mendes de Jesus, J. (2017). WoSIS: Providing standardised soil profile data for the world. *Earth System Science Data*, *9*(1), 1–14. https://doi.org/10.5194/essd-9-1-2017

Bell, R. V. (1971). A Grazing Ecosystem in the Serengeti. *Scientific American*, *225*(1), 86–93.

Berger, J. (2004). The Last Mile: How to Sustain Long-Distance Migration in Mammals. *Conservation Biology*, *18*(2), 320–331.

Bergesen, H. O., Parmann, G., & Thommessen, Ø. B. (Eds.). (2018). Convention on the Conservation of Migratory Species of Wild Animals (CMS). In H. O. Bergesen, G. Parmann, & O. B. Thommessen, *Yearbook of International Cooperation on Environment and Development 1998–99* (1st ed., pp. 154–155). Routledge. https://doi.org/10.4324/9781315066547-40

Bhat, U., Kempes, C. P., & Yeakel, J. D. (2020). Scaling the risk landscape drives optimal life-history strategies and the evolution of grazing. *Proceedings of the National Academy of Sciences*, *117*(3), 1580–1586. https://doi.org/10.1073/pnas.1907998117

Bolger, D. T., Morrison, T. A., & Doak, D. F. (2007). *The need for integrative approaches to understand and conserve migratory ungulates*. 15.

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a Metabolic Theory of Ecology. *Ecology*, *85*(7), 1771–1789. https://doi.org/10.1890/03-9000

Cardillo, M., Mace, G. M., Jones, K. E., Bielby, J., Bininda-Emonds, O. R. P., Sechrest, W., Orme, C. D. L., & Purvis, A. (2005). Multiple Causes of High Extinction Risk in Large Mammal Species. *Science*, *309*(5738), 1239–1241. https://doi.org/10.1126/science.1116030

Codron, D., Codron, J., Lee-Thorp, J. A., Sponheimer, M., Ruiter, D. D., Sealy, J., Grant, R., & Fourie, N. (2007). Diets of savanna ungulates from stable carbon isotope composition of faeces. *Journal of Zoology*, *273*(1), 21–29. https://doi.org/10.1111/j.1469-7998.2007.00292.x

Cote, J., Bocedi, G., Debeffe, L., Chudzińska, M. E., Weigang, H. C., Dytham, C., Gonzalez, G., Matthysen, E., Travis, J., Baguette, M., & Hewison, A. J. M. (2017). Behavioural synchronization of large-scale animal movements—Disperse alone, but migrate together?: Synchronization of large-scale animal movements. *Biological Reviews*, *92*(3), 1275–1296. https://doi.org/10.1111/brv.12279

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D., Jackson, J. B. C., Marquis, R. J., Oksanen, L., Oksanen, T., Paine, R. T., Pikitch, E. K., Ripple, W. J., Sandin, S. A., Scheffer, M., Schoener, T. W., … Wardle, D. A. (2011). Trophic Downgrading of Planet Earth. *Science*, *333*(6040), 301–306. https://doi.org/10.1126/science.1205106

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, *37*(12), 4302–4315. https://doi.org/10.1002/joc.5086

Freckleton, R. P., Harvey, P. H., & Pagel, M. (2003). Bergmann's Rule and Body Size in Mammals. *The American Naturalist*, *161*(5), 821–825. https://doi.org/10.1086/374346

Fryxell, J. M., & Sinclair, A. R. E. (1988). Causes and consequences of migration by large herbivores. *Trends in Ecology & Evolution*, *3*(9), 237–241. https://doi.org/10.1016/0169-5347(88)90166-8

Gagnon, M., & Chew, A. E. (2000). Dietary Preferences in Extant African Bovidae. *Journal of Mammalogy*, *81*(2), 490–511. https://doi.org/10.1644/1545-1542(2000)081<0490:DPIEAB>2.0.CO;2

Garland, T., Jr., Dickerman, A. W., Janis, C. M., & Jones, J. A. (1993). Phylogenetic Analysis of Covariance by Computer Simulation. *Systematic Biology*, *42*(3), 265–292. https://doi.org/10.1093/sysbio/42.3.265

Güsewell, S. (2004). N: P ratios in terrestrial plants: variation and functional significance. *New Phytologist*, *164*(2), 243–266. https://doi.org/10.1111/j.1469-8137.2004.01192.x

Harris, G., Thirgood, S., Hopcraft, J. G. C., Cromsigt, J. P. G. M., & Berger, J. (2009). Global decline in aggregated migrations of large terrestrial mammals. *Endangered Species Research*, *7*(1), 55–76. https://doi.org/10.3354/esr00173

Hein, A. M., Hou, C., & Gillooly, J. F. (2012). Energetic and biomechanical constraints on animal migration distance. *Ecology Letters*, *15*(2), 104–110. https://doi.org/10.1111/j.1461-0248.2011.01714.x

Hempson, G. P., Archibald, S., & Bond, W. J. (2015). A continent-wide assessment of the form and intensity of large mammal herbivory in Africa. *Science*, *350*(6264), 1056–1061. https://doi.org/10.1126/science.aac7978

Holdo, R. M., Holt, R. D., & Fryxell, J. M. (2009). Opposing Rainfall and Plant Nutritional Gradients Best Explain the Wildebeest Migration in the Serengeti. *The American Naturalist*, *173*(4), 431–445. https://doi.org/10.1086/597229

Hopcraft, J. G. C., Holdo, R. M., Mwangomo, E., Mduma, S. A. R., Thirgood, S. J., Borner, M., Fryxell, J. M., Olff, H., & Sinclair, A. R. E. (2015). 6. Why Are Wildebeest the Most Abundant Herbivore in the Serengeti Ecosystem? In *Serengeti IV: Sustaining Biodiversity in a Coupled Human-Natural System* (pp. 125–174). University of Chicago Press. https://doi.org/10.7208/9780226196336-007

Hopcraft, J. G. C., Olff, H., & Sinclair, A. R. E. (2010). Herbivores, resources and risks: Alternating regulation along primary environmental gradients in savannas. *Trends in Ecology & Evolution*, *25*(2), 119–128. https://doi.org/10.1016/j.tree.2009.08.001

Illius, A. W., & O’Connor, T. G. (2000). Resource heterogeneity and ungulate population dynamics. *Oikos*, *89*(2), 283–294. https://doi.org/10.1034/j.1600-0706.2000.890209.x

IUCN. (2019). *The IUCN Red List of Threatened Species*. IUCN Red List of Threatened Species. https://www.iucnredlist.org/en

Janis, C. M. (1993). Tertiary Mammal Evolution in the Context of Changing Climates, Vegetation, and Tectonic Events. *Annual Review of Ecology and Systematics*, *24*, 467–500.

Janis, C. M. (2008). An Evolutionary History of Browsing and Grazing Ungulates. In I. J. Gordon & H. H. T. Prins (Eds.), *The Ecology of Browsing and Grazing* (pp. 21–45). Springer. https://doi.org/10.1007/978-3-540-72422-3_2

Jarman, P. J. (1974). The Social Organisation of Antelope in Relation To Their Ecology. *Behaviour*, *48*(1–4), 215–267. https://doi.org/10.1163/156853974X00345

Joly, K., Gurarie, E., Sorum, M. S., Kaczensky, P., Cameron, M. D., Jakes, A. F., Borg, B. L., Nandintsetseg, D., Hopcraft, J. G. C., Buuveibaatar, B., Jones, P. F., Mueller, T., Walzer, C., Olson, K. A., Payne, J. C., Yadamsuren, A., & Hebblewhite, M. (2019). Longest terrestrial migrations and movements around the world. *Scientific Reports*, *9*(1), 15333. https://doi.org/10.1038/s41598-019-51884-5

Kartzinel, T. R., & Pringle, R. M. (2020). Multiple dimensions of dietary diversity in large mammalian herbivores. *Journal of Animal Ecology*, *89*(6), 1482–1496. https://doi.org/10.1111/1365-2656.13206

Kaufmann, J. H. (1974). The Ecology and Evolution of Social Organization in the Kangaroo Family (Macropodidae). *American Zoologist*, *14*(1), 51–62. https://doi.org/10.1093/icb/14.1.51

Lindenfors, P., Revell, L. J., & Nunn, C. L. (2010). Sexual dimorphism in primate aerobic capacity: A phylogenetic test. *Journal of Evolutionary Biology*, *23*(6), 1183–1194. https://doi.org/10.1111/j.1420-9101.2010.01983.x

McGowan, C. P., Skinner, J., & Biewener, A. A. (2008). Hind limb scaling of kangaroos and wallabies (superfamily Macropodoidea): Implications for hopping performance, safety factor and elastic savings. *Journal of Anatomy*, *212*(2), 153–163. https://doi.org/10.1111/j.1469-7580.2007.00841.x

Olff, H., Ritchie, M. E., & Prins, H. H. T. (2002). Global environmental controls of diversity in large herbivores. *Nature*, *415*(6874), 901–904. https://doi.org/10.1038/415901a

Paradis, E., Claude, J., & Strimmer, K. (2004). APE: Analyses of Phylogenetics and Evolution in R language. *Bioinformatics*, *20*(2), 289–290. https://doi.org/10.1093/bioinformatics/btg412

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & Team, R. C. (2007). Linear and nonlinear mixed effects models. *R Package Version*, *3*(57), 1–89.

R Core Team. (2020). *R: A language and environment for statistical computing.* (3.6.1) [Computer software]. R Foundation for Statistical Computing.

Reich, P. B., & Oleksyn, J. (2004). Global patterns of plant leaf N and P in relation to temperature and latitude. *Proceedings of the National Academy of Sciences*, *101*(30), 11001–11006. https://doi.org/10.1073/pnas.0403588101

Revell, L. J. (2012). phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, *3*(2), 217–223. https://doi.org/10.1111/j.2041-210X.2011.00169.x

Ripple, W. J., Newsome, T. M., Wolf, C., Dirzo, R., Everatt, K. T., Galetti, M., Hayward, M. W., Kerley, G. I. H., Levi, T., Lindsey, P. A., Macdonald, D. W., Malhi, Y., Painter, L. E., Sandom, C. J., Terborgh, J., & Van Valkenburgh, B. (2015). Collapse of the world's largest herbivores. *Science Advances*, *1*(4), e1400103. https://doi.org/10.1126/sciadv.1400103

Running, S. W., Nemani, R. R., Heinsch, F. A., Zhao, M., Reeves, M., & Hashimoto, H. (2004). A Continuous Satellite-Derived Measure of Global Terrestrial Primary Production. *BioScience*, *54*(6), 547–560. https://doi.org/10.1641/0006-3568(2004)054[0547:ACSMOG]2.0.CO;2

Ryan, C. M., Williams, M., Grace, J., Woollen, E., & Lehmann, C. E. R. (2017). Pre-rain green-up is ubiquitous across southern tropical Africa: Implications for temporal niche separation and model representation. *New Phytologist*, *213*(2), 625–633. https://doi.org/10.1111/nph.14262

Scanlon, T. M., Caylor, K. K., Manfreda, S., Levin, S. A., & Rodriguez-Iturbe, I. (2005). Dynamic response of grass cover to rainfall variability: Implications for the function and persistence of savanna ecosystems. *Advances in Water Resources*, *28*(3), 291–302. https://doi.org/10.1016/j.advwatres.2004.10.014

Schowanek, S. D., Davis, M., Lundgren, E. J., Middleton, O., Rowan, J., Pedersen, R. Ø., Ramp, D., Sandom, C. J., & Svenning, J.-C. (2021). Reintroducing extirpated herbivores could partially reverse the late Quaternary decline of large and grazing species. *Global Ecology and Biogeography*, *30*(4), 896–908. https://doi.org/10.1111/geb.13264

Scott, K. M. (Kathleen M. (1985). *Allometric trends and locomotor adaptations in the Bovidae. Bulletin of the AMNH ; v. 179, article 2*. https://digitallibrary.amnh.org/handle/2246/1005

Shaw, A. K. (2016). Drivers of animal migration and implications in changing environments. *Evolutionary Ecology*, *30*(6), 991–1007. https://doi.org/10.1007/s10682-016-9860-5

Singh, N. J., Börger, L., Dettki, H., Bunnefeld, N., & Ericsson, G. (2012). From migration to nomadism: Movement variability in a northern ungulate across its latitudinal range. *Ecological Applications*, *22*(7), 2007–2020. https://doi.org/10.1890/12-0245.1

Smith, F. A., Boyer, A. G., Brown, J. H., Costa, D. P., Dayan, T., Ernest, S. K. M., Evans, A. R., Fortelius, M., Gittleman, J. L., Hamilton, M. J., Harding, L. E., Lintulaakso, K., Lyons, S. K., McCain, C., Okie, J. G., Saarinen, J. J., Sibly, R. M., Stephens, P. R., Theodor, J., & Uhen, M. D. (2010). The Evolution of Maximum Body Size of Terrestrial Mammals. *Science*, *330*(6008), 1216–1219. https://doi.org/10.1126/science.1194830

Staver, A. C., Abraham, J. O., Hempson, G. P., Karp, A. T., & Faith, J. T. (2021). The past, present, and future of herbivore impacts on savanna vegetation. *Journal of Ecology*, *109*(8), 2804–2822. https://doi.org/10.1111/1365-2745.13685

Staver, A. C., & Hempson, G. P. (2020). Seasonal dietary changes increase the abundances of savanna herbivore species. *Science Advances*, *6*(40), eabd2848. https://doi.org/10.1126/sciadv.abd2848

Toljagić, O., Voje, K. L., Matschiner, M., Liow, L. H., & Hansen, T. F. (2018). Millions of Years Behind: Slow Adaptation of Ruminants to Grasslands. *Systematic Biology*, *67*(1), 145–157. https://doi.org/10.1093/sysbio/syx059

Upham, N. S., Esselstyn, J. A., & Jetz, W. (2019). Inferring the mammal tree: Species-level sets of phylogenies for questions in ecology, evolution, and conservation. *PLOS Biology*, *17*(12), e3000494. https://doi.org/10.1371/journal.pbio.3000494

Veldhuis, M. P., Kihwele, E. S., Cromsigt, J. P. G. M., Ogutu, J. O., Hopcraft, J. G. C., Owen-Smith, N., & Olff, H. (2019). Large herbivore assemblages in a changing climate: Incorporating water dependence and thermoregulation. *Ecology Letters*, ele.13350. https://doi.org/10.1111/ele.13350

Walker, E. P., Warnick, F., Hamlet, S. E., Lange, K. I., Davis, M. A., Uible, H. E., Wright, P. F., & Paradiso, J. L. (1968). *Mammals of the world* (1st ed.). Johns Hopkins University Press.

Webber, Q. M. R., & McGuire, L. P. (2021). Heterothermy, body size, and locomotion as ecological predictors of migration in mammals. *Mammal Review*, *n/a*(n/a). https://doi.org/10.1111/mam.12263

Wilman, H., Belmaker, J., Simpson, J., Rosa, C. de la, Rivadeneira, M. M., & Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology*, *95*(7), 2027–2027. https://doi.org/10.1890/13-1917.1

Xu, L., Myneni, R. B., Chapin III, F. S., Callaghan, T. V., Pinzon, J. E., Tucker, C. J., Zhu, Z., Bi, J., Ciais, P., Tømmervik, H., Euskirchen, E. S., Forbes, B. C., Piao, S. L., Anderson, B. T., Ganguly, S., Nemani, R. R., Goetz, S. J., Beck, P. S. A., Bunn, A. G., … Stroeve, J. C. (2013). Temperature and vegetation seasonality diminishment over northern lands. *Nature Climate Change*, *3*(6), 581–586. https://doi.org/10.1038/nclimate1836

TABLES

Table 1. Directions for future research.

Mechanism underlying Jarman-Bell: Though we recovered support for increasing grass consumption with larger body size, consistent with the Jarman-Bell Principle, the underlying mechanisms for Jarman-Bell remain unclear: the Jarman-Bell Principle may result from sub-unity scaling of metabolism with body size, larger gut capacities and longer gut retention times of large herbivores, or the scaling of resource distributions with body size (Bell, 1971; Bhat *et al.,* 2020; Jarman, 1974). Additionally, we found substantial variation in grass dependency not explained by body size. *What mechanism underlies the Jarman-Bell Principle? And what determines the large variability in grass dependence not explained by body size?*
Evolutionary links between body size, grass consumption, and migration: Body size, grass dependence, and migration were all interrelated: large herbivores consumed more grass and migrated more, and migratory herbivores ate more grass. *How does the timing of body size evolution in mammalian herbivores relate to the expansion of grasslands since the late Miocene? Was the expansion of grasslands related to the evolution of migratory strategies? Is migration related to body size evolution of mammals through the Cenozoic?*
Migration and the Pleistocene megafaunal extinctions: Large-bodied animals disproportionately went extinct during the late Pleistocene (Barnosky, 2004). We found that the largest extant herbivores were disproportionately migratory. Furthermore, contemporary migratory collapse has driven many large herbivores closer to extinction (Harris *et al.,* 2009). *Was migration prevalent among now-extinct Pleistocene megafauna? Did the disruption of migratory pathways—by human impacts or climate-driven environmental changes—contribute to to the demise of Pleistocene megafauna?*
History and cost of mixed feeding: Mixed feeding herbivores sustain larger population sizes than their specialist counterparts (Staver & Hempson, 2020), despite presumed energetic costs of generalism (*e.g.,* constraints on bite size and/or digestive efficiency). However, we found that mixed feeder diversity was low. *Were mixed feeders dominant historically, as they are today? Or was mixed feeding a less beneficial strategy in the past, when ecosystems were grassier? Does this account for their low diversity?*
Magnitudes and mechanisms of seasonal diet shifts: Observed seasonal diet shifts were of smaller magnitude than expected, peaking at *ca.* 20%. *What constrains the magnitude of seasonal diet shifts? How and at what scale do mixed feeders select for resources?*
Latitudinal gradients in herbivore impacts: Extratropical herbivores were less diverse than tropical ones, exhibited more intermediate phenotypes, and were likelier to migrate and diet switch seasonally. *Are seasonal resource bottlenecks more extreme outside of the tropics because forage seasonality is uniform across plant functional types? Does reduced seasonality in the tropics translate to higher herbivore population densities, and resultantly larger herbivore impacts?*

FIGURES

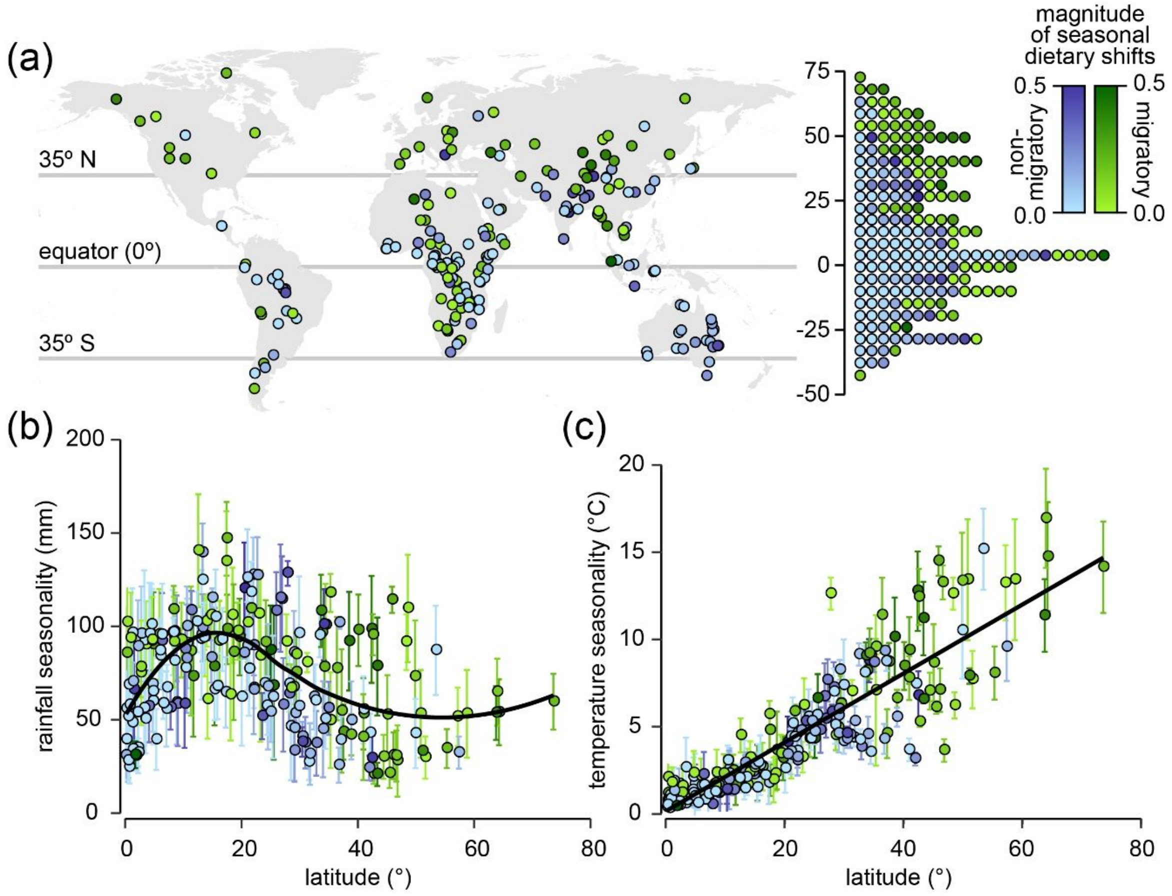

Figure 1. The global distribution of herbivores (*a*) and relationships between rainfall seasonality and latitude (*b*) and temperature seasonality and latitude (*c*) across herbivore species' ranges. Points in (*a*) correspond to species range centroids. Herbivores are distributed across every continent excluding Antarctica and experience a wide range of seasonally variable conditions. Point and error bar colors correspond to herbivore strategies, where *blue* corresponds to non-migratory herbivores, *green* corresponds to migratory herbivores, and *darker* colors reflect species that exhibit larger seasonal diet shifts. Note that migration is coded as a binary whereas diet shifts take proportional values.

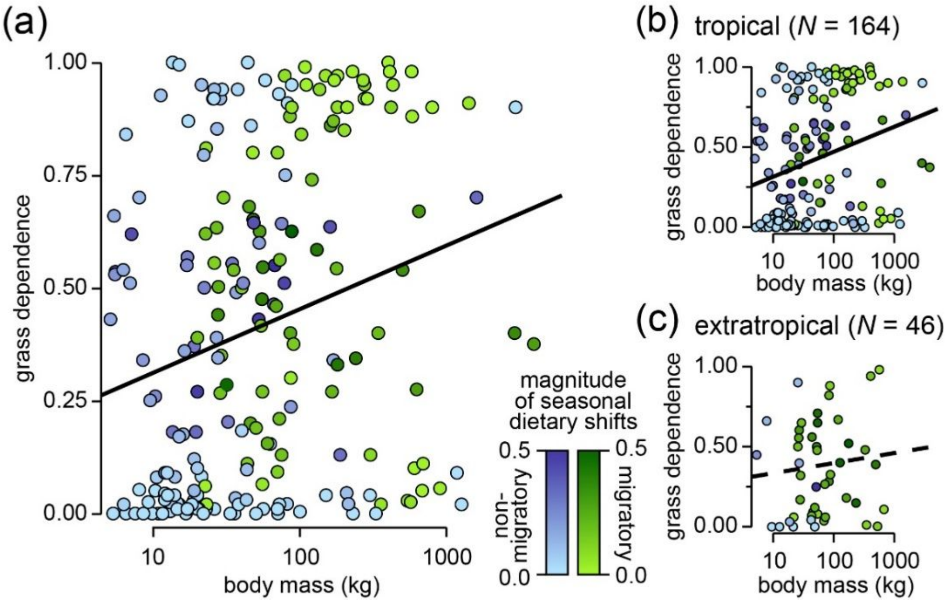

Figure 2. The relationship between herbivore body mass and grass dependence across all herbivores (*a*; $N = 210$), across tropical herbivores (*b; N* =164), and across extratropical herbivores (*c; N* = 46). Body mass was positively correlated with grass consumption in the global dataset, but this relationship broke down when only extratropical herbivores were considered. Point colors correspond to herbivore strategies, where *blue* points correspond to non-migratory herbivores, *green* points correspond to migratory herbivores, and *darker* points reflect species that exhibit larger seasonal diet shifts. *Solid* regression lines indicate significant relationships ($P < 0.05$), and a *dashed* line indicates a non-significant relationship ($P \geq 0.05$).

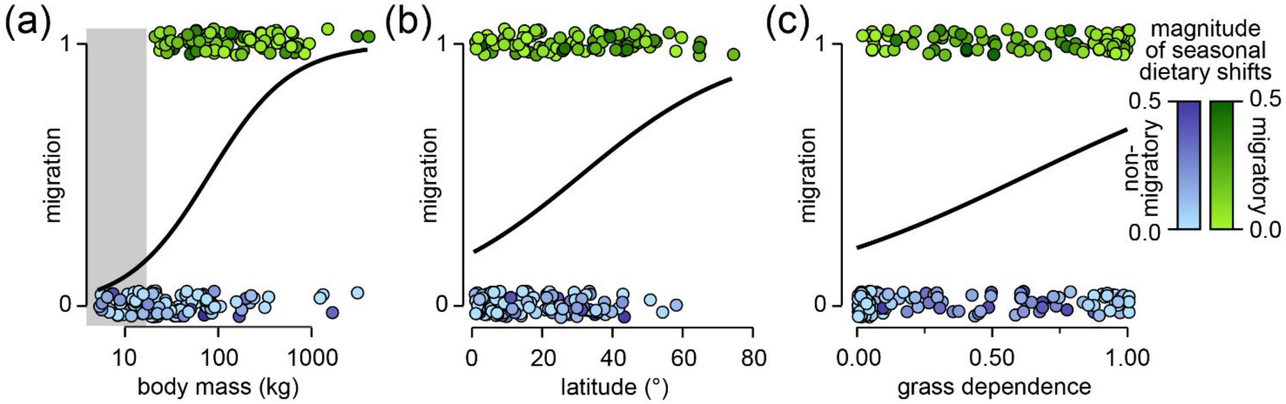

Figure 3. Relationships between migration and body mass (*a*), latitude (*b*), and grass dependence (*c*). All three were positively correlated with migratory behavior in herbivores. Point colors correspond to herbivore strategies, where *blue* points correspond to non-migratory herbivores, *green* points correspond to migratory herbivores, and *darker* points reflect species that exhibit larger seasonal diet shifts. The *light grey* box in (*a*) corresponds to the region of trait space where no herbivores exhibit migratory behavior, possibly suggesting energetic constraints on migration. *Solid* regression lines indicate significant relationships ($P < 0.05$).

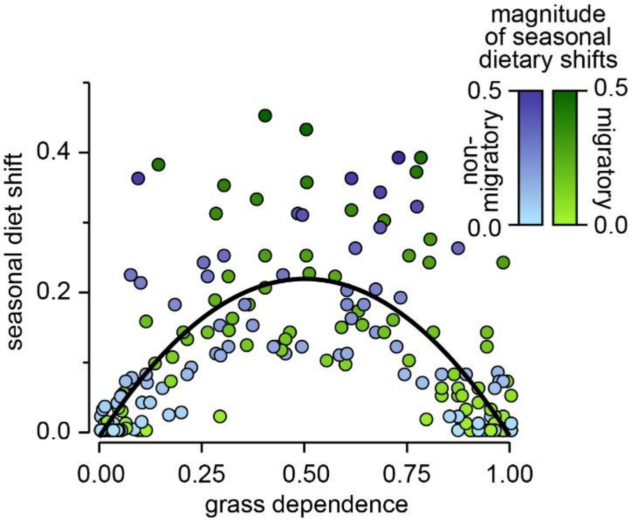

Figure 4. The relationship between herbivore grass dependence and the magnitude of seasonal dietary shifts. Dietary shifts peaked at intermediate grass dependences. Point colors correspond to herbivore strategies, where *blue* points correspond to non-migratory herbivores, *green* points correspond to migratory herbivores, and *darker* points reflect species that exhibit larger seasonal diet shifts. The *solid* regression line indicates a significant relationship ($P < 0.05$).

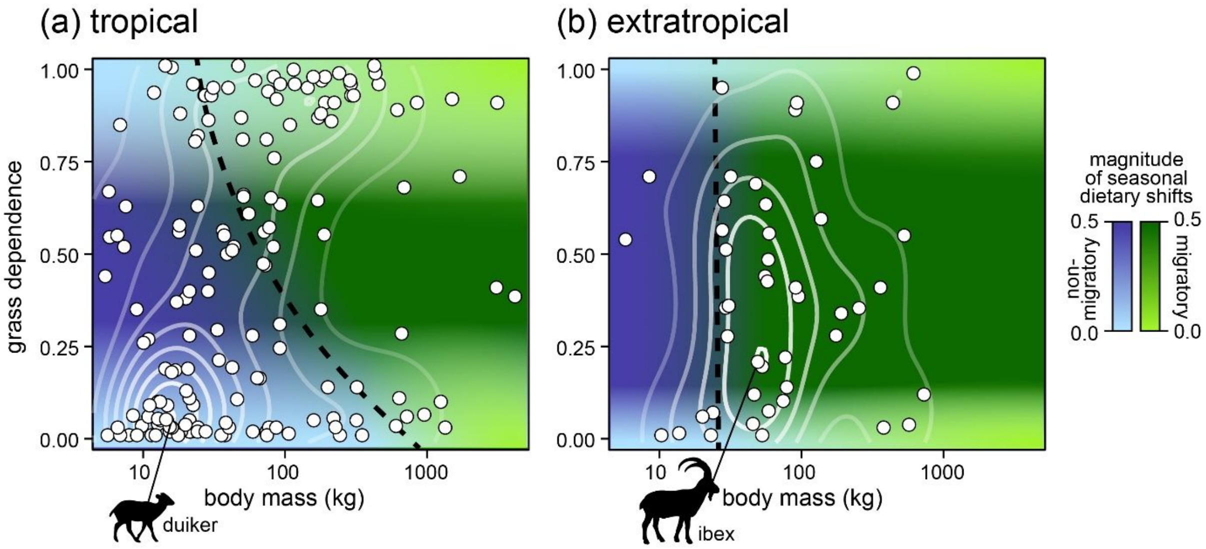

Figure 5. *Conceptual synthesis***.** Strategies for navigating scarcity in the tropics are most prevelant among grass-dependent herbivores and large herbivores with bulky forage requirements, whereas nearly all extratropical herbivores exhibit one or both seasonal strategies. These latitudinal differences in the distribution of strategies are likely because only grass forage is seasonally available in the tropics, whereas all vegetation is strongly seasonal in the extratropics. Inconsistent resource availability may also preclude dietary specialists in extratropical systems, while forage and thermoregulatory requirements likely restrict extratropical herbivores to more intermediate body sizes. Contrastingly, in the tropics there is a much higher diversity of specialist herbivores (and herbivores more generally), with comparatively few generalists. Herbivore trait space is colored according to the distribution of different strategies: *blue* corresponds to non-migratory herbivores, *green* corresponds to migratory herbivores, and *darker* colors reflect regions of trait space where larger seasonal diet shifts are expected. *White* contours indicate how herbivores are distributed in trait space, with the most representative herbivore from tropical and extratropical environments respectively depicted in silhouette. *Black* dashed lines correspond to the migration threshold in each environment, below which few herbivores exhibit migration.

MANUSCRIPT TITLE: Seasonal strategies differ between tropical and extratropical herbivores

AUTHORS: Joel O. Abraham, Gareth P. Hempson, J. Tyler Faith, and A. Carla Staver

SUPPORTING INFORMATION

Table S1. Complete list of all 210 herbivorous mammals included in this study, representing 7 orders and 23 families distributed across the globe, as well as their range centroids, body masses, seasonal grass dependences, and migratory status.

Scientific name	Family	Latitude	Longitude	Body mass	Growing season dietary grass	Dormant season dietary grass	Avg. dietary grass	Dietary sources	Migration	Migration sources
Addax nasomaculatus	Bovidae	17.4	7.7	70.0	0.83	0.77	0.80	*58, 62*	1	*31*
Aepyceros melampus	Bovidae	-13.3	31.6	52.5	0.67	0.53	0.60	*32*	1	*169*
Ailuropoda melanoleuca	Ursidae	31.3	104.1	108.4	0.99	0.99	0.99	*131*	1	*177*
Alcelaphus buselaphus	Bovidae	-4.6	21.0	171.0	0.96	0.97	0.96	*193*	1	*20*
Alces alces	Cervidae	58.8	43.2	357.0	0.04	0.01	0.02	*127*	1	*127*
Alces americanus	Cervidae	50.8	-72.4	541.5	0.06	0.00	0.03	*88*	1	*162*
Ammotragus lervia	Bovidae	25.5	4.7	48.0	0.78	0.39	0.65	*125*	1	*31*
Antidorcas marsupialis	Bovidae	-25.0	20.9	31.5	0.50	0.07	0.29	*150*	1	*20*
Antilocapra americana	Antilocapridae	41.0	-106.3	46.1	0.31	0.09	0.20	*153*	1	*145*
Antilope cervicapra	Bovidae	21.0	77.4	37.5	0.95	0.93	0.94	*76*	0	*84*
Axis axis	Cervidae	20.5	79.6	67.3	0.73	0.34	0.55	*95*	0	*95*
Axis porcinus	Cervidae	26.0	87.3	34.4	0.44	0.67	0.55	*46, 178*	0	*46*
Beatragus hunteri	Bovidae	-1.3	40.5	79.1	0.78	0.72	0.75	*8*	0	*8*
Bison bison	Bovidae	57.2	-120.5	579.3	0.98	0.98	0.98	*35*	1	*20*
Bison bonasus	Bovidae	51.1	23.2	500.0	0.69	0.39	0.54	*107*	1	*139*
Blastocerus dichotomus	Cervidae	-18.1	-54.3	86.7	0.29	0.31	0.30	*170*	1	*170*
Bos gaurus	Bovidae	19.7	93.6	650.0	0.80	0.53	0.67	*29*	1	*4*
Bos javanicus	Bovidae	11.7	106.5	625.0	0.40	0.15	0.28	*21*	1	*172*
Bos mutus	Bovidae	35.3	86.9	416.5	0.86	0.94	0.90	*72, 123*	1	*31*
Bos sauveli	Bovidae	13.7	106.1	800.0	0.90	0.90	0.90	*180*	1	*31*
Boselaphus tragocamelus	Bovidae	22.7	78.5	169.0	0.28	0.39	0.34	*13*	0	*95*
Bubalus arnee	Bovidae	21.1	94.0	431.3	0.96	0.94	0.95	*39*	1	*173*
Bubalus depressicornis	Bovidae	-1.9	121.4	300.0	0.04	0.04	0.04	*142*	0	*142*

Bubalus quarlesi	Bovidae	-2.3	120.8	150.0	0.04	0.04	0.04	*142*	0	*142*
Budorcas taxicolor	Bovidae	29.4	99.0	302.0	0.17	0.10	0.13	*147*	1	*147*
Camelus bactrianus	Camelidae	48.3	95.9	690.0	0.11	0.11	0.11	*81*	1	*31*
Camelus dromedarius	Camelidae	27.7	22.4	601.0	0.10	0.10	0.10	*81*	1	*31*
Capra caucasica	Bovidae	43.3	41.7	55.0	0.30	0.65	0.48	*179*	1	*179*
Capra cylindricornis	Bovidae	42.1	46.0	50.0	0.00	0.00	0.00	*12*	0	*12*
Capra falconeri	Bovidae	35.0	72.1	41.0	0.60	0.42	0.51	*3*	0	*17*
Capra ibex	Bovidae	45.5	7.1	85.2	0.94	0.82	0.88	*137*	1	*137*
Capra nubiana	Bovidae	24.0	40.4	62.6	0.17	0.14	0.15	*71*	0	*198*
Capra pyrenaica	Bovidae	38.9	-2.4	50.0	0.26	0.12	0.19	*64*	1	*2*
Capra sibirica	Bovidae	43.3	86.3	130.0	0.77	0.40	0.59	*57*	1	*57*
Capra walie	Bovidae	13.3	38.2	100.0	0.01	0.00	0.00	*66*	0	*52*
Capreolus capreolus	Cervidae	51.6	20.5	22.5	0.06	0.06	0.06	*127*	1	*127*
Capreolus pygargus	Cervidae	49.8	98.5	43.8	0.17	0.07	0.11	*9*	1	*73*
Capricornis crispus	Bovidae	37.1	138.6	43.0	0.01	0.04	0.03	*133*	0	*100*
Capricornis sumatraensis	Bovidae	1.7	100.1	87.5	0.40	0.85	0.63	*179*	1	*179*
Castor canadensis	Castoridae	49.9	-106.3	21.8	0.00	0.00	0.00	*25*	0	*25*
Castor fiber	Castoridae	57.4	35.7	19.0	0.11	0.03	0.05	*101*	0	*101*
Catagonus wagneri	Tayassuidae	-22.1	-61.3	35.6	0.00	0.00	0.00	*118*	0	*118*
Cephalophus adersi	Bovidae	-4.6	38.8	9.2	0.03	0.03	0.03	*62*	0	*198*
Cephalophus callipygus	Bovidae	0.8	13.5	18.2	0.02	0.02	0.02	*62*	0	*198*
Cephalophus dorsalis	Bovidae	0.2	14.6	20.0	0.04	0.04	0.04	*26*	0	*198*
Cephalophus harveyi	Bovidae	-6.0	36.4	14.5	0.01	0.01	0.01	*26*	0	*198*
Cephalophus jentinki	Bovidae	6.5	-8.8	70.0	0.01	0.01	0.01	*62*	0	*198*
Cephalophus leucogaster	Bovidae	0.5	17.4	12.7	0.04	0.04	0.04	*26*	0	*198*
Cephalophus natalensis	Bovidae	-16.7	36.1	12.0	0.03	0.03	0.03	*26*	0	*198*
Cephalophus niger	Bovidae	7.2	-4.3	20.4	0.01	0.01	0.01	*62*	0	*198*
Cephalophus nigrifrons	Bovidae	-2.2	19.9	13.9	0.04	0.04	0.04	*26*	0	*198*
Cephalophus ogilbyi	Bovidae	4.8	5.9	20.0	0.01	0.01	0.01	*62*	0	*198*
Cephalophus rufilatus	Bovidae	8.9	6.6	12.0	0.18	0.00	0.09	*48*	0	*198*
Cephalophus silvicultor	Bovidae	-0.6	15.8	72.5	0.02	0.02	0.02	*26*	0	*198*
Cephalophus spadix	Bovidae	-6.1	36.8	56.0	0.01	0.01	0.01	*62*	0	*198*
Cephalophus weynsi	Bovidae	-0.2	24.2	17.0	0.01	0.01	0.01	*62*	0	*198*
Cephalophus zebra	Bovidae	6.5	-8.8	17.5	0.01	0.01	0.01	*62*	0	*198*

Ceratotherium simum	Rhinocerotidae	3.3	25.3	2950.0	0.90	0.90	0.90	*33*	0	*176*
Cervus albirostris	Cervidae	33.8	97.8	161.7	0.98	0.74	0.86	*72, 164*	1	*72*
Cervus elaphus	Cervidae	46.1	48.7	165.0	0.36	0.18	0.27	*28*	1	*31*
Cervus nippon	Cervidae	37.5	140.0	53.0	0.75	0.50	0.63	*165*	1	*20*
Connochaetes gnou	Bovidae	-29.0	26.3	180.0	0.97	0.97	0.97	*62*	1	*73*
Connochaetes taurinus	Bovidae	-19.4	24.8	180.0	0.87	0.92	0.90	*33*	1	*73*
Dama dama	Cervidae	42.5	19.5	52.4	0.61	0.25	0.43	*82*	0	*168*
Damaliscus lunatus	Bovidae	-9.7	25.5	136.0	0.92	0.98	0.94	*33*	1	*73*
Damaliscus pygargus	Bovidae	-28.5	27.3	102.0	0.87	0.81	0.84	*90*	1	*73*
Dicerorhinus sumatrensis	Rhinocerotidae	2.2	103.1	1266.7	0.02	0.02	0.02	*144*	0	*176*
Diceros bicornis	Rhinocerotidae	-13.2	26.1	1180.5	0.09	0.09	0.09	*33*	0	*176*
Dinomys branickii	Dinomyidae	-5.3	-71.7	12.5	0.04	0.04	0.04	*67*	0	*67*
Dolichotis patagonum	Caviidae	-38.9	-67.5	8.0	0.74	0.66	0.70	*155*	0	*155*
Dorcatragus megalotis	Bovidae	10.4	46.9	10.2	0.05	0.05	0.05	*62*	0	*198*
Elaphodus cephalophus	Cervidae	28.2	108.5	33.5	0.00	0.00	0.00	*109*	0	*109*
Elephas maximus	Elephantidae	15.3	98.1	2915.0	0.61	0.30	0.40	*140*	1	*87*
Equus burchellii	Equidae	14.2	40.4	276.0	0.92	0.92	0.92	*33*	1	*31*
Equus grevyi	Equidae	3.6	39.8	408.0	0.98	0.98	0.98	*91*	1	*196*
Equus hemionus	Equidae	42.4	97.4	240.0	0.50	0.15	0.34	*188*	1	*31*
Equus kiang	Equidae	34.5	88.9	275.0	0.99	0.92	0.95	*72, 191*	1	*31*
Equus quagga	Equidae	-13.7	29.9	400.0	1.00	1.00	1.00	*49*	1	*73*
Equus zebra	Equidae	-23.0	16.4	287.0	0.92	0.92	0.92	*183*	1	*19*
Eudorcas rufifrons	Bovidae	13.3	12.5	27.0	0.45	0.34	0.39	*62, 148*	0	*198*
Eudorcas thomsonii	Bovidae	-2.7	35.9	22.9	0.83	0.78	0.81	*193*	1	*31*
Gazella arabica	Bovidae	21.3	45.7	12.0	0.04	0.04	0.04	*186*	0	*186*
Gazella bennettii	Bovidae	26.7	68.3	18.9	0.26	0.48	0.37	*13*	0	*5*
Gazella dorcas	Bovidae	23.2	11.5	23.0	0.02	0.03	0.02	*14*	1	*31*
Gazella gazella	Bovidae	21.7	46.7	22.7	0.69	0.55	0.62	*14*	1	*31*
Gazella leptoceros	Bovidae	27.2	10.0	22.2	0.60	0.40	0.50	*89, 62, 34*	0	*198*
Gazella spekei	Bovidae	8.3	48.5	20.0	0.46	0.32	0.39	*98, 47, 62*	1	*15*
Gazella subgutturosa	Bovidae	36.4	69.0	28.5	0.31	0.17	0.27	*188*	1	*31*
Giraffa camelopardalis	Giraffidae	-8.5	28.2	900.0	0.06	0.05	0.06	*33*	1	*31*
Hemitragus jemlahicus	Bovidae	29.4	82.9	35.2	0.59	0.44	0.54	*68*	1	*68*
Hippocamelus antisensis	Cervidae	-17.5	-69.9	68.6	0.57	0.35	0.46	*65, 16*	1	*19, 16*

Hippocamelus bisulcus	Cervidae	-46.8	-72.8	70.0	0.13	0.04	0.09	*63*	1	*31*
Hippopotamus amphibius	Hippopotamidae	-5.9	25.1	1417.5	0.89	0.92	0.91	*33*	1	*119, 132, 53, 169, 174*
Hippotragus equinus	Bovidae	-0.4	18.1	270.0	0.95	0.98	0.96	*33*	1	*7*
Hippotragus niger	Bovidae	-14.0	31.3	227.5	0.98	0.98	0.98	*33*	1	*169, 61*
Hydrochoerus hydrochaeris	Caviidae	-10.2	-57.6	48.1	0.49	0.80	0.65	*45*	0	*45*
Hydropotes inermis	Cervidae	32.5	121.2	14.0	0.11	0.04	0.08	*97*	0	*97*
Hyemoschus aquaticus	Tragulidae	1.3	16.0	10.9	0.00	0.00	0.00	*51*	0	*198*
Hylochoerus meinertzhageni	Suidae	4.1	14.9	188.5	0.25	0.01	0.13	*195*	0	*195*
Hystrix cristata	Hystricidae	10.6	16.7	16.3	0.42	0.30	0.36	*24*	0	*198*
Hystrix indica	Hystricidae	29.9	64.2	12.4	0.10	0.09	0.09	*6*	0	*6*
Kobus ellipsiprymnus	Bovidae	-1.0	22.9	210.0	0.89	0.90	0.90	*33*	1	*184, 169*
Kobus kob	Bovidae	8.4	12.5	78.5	1.00	0.95	0.97	*48*	1	*31*
Kobus leche	Bovidae	-14.8	23.2	110.7	0.95	0.95	0.95	*62, 134*	1	*192*
Kobus megaceros	Bovidae	8.3	30.9	87.5	0.95	0.95	0.95	*62*	0	*198*
Kobus vardonii	Bovidae	-12.3	26.8	71.5	0.93	0.93	0.93	*62, 134*	0	*198*
Lama guanicoe	Camelidae	-37.2	-68.2	120.0	0.81	0.67	0.74	*141*	1	*143*
Lasiorhinus latifrons	Vombatidae	-31.6	131.8	25.5	0.92	0.92	0.92	*185*	0	*185*
Litocranius walleri	Bovidae	4.5	42.6	38.0	0.02	0.02	0.02	*26*	0	*198*
Loxodonta africana	Elephantidae	-4.9	23.9	3940.0	0.50	0.25	0.38	*32*	1	*194*
Macropus agilis	Macropodidae	-15.5	135.4	15.0	1.00	0.99	1.00	*10*	0	*198*
Macropus antilopinus	Macropodidae	-15.0	133.7	27.3	0.89	0.81	0.85	*10*	0	*198*
Macropus dorsalis	Macropodidae	-25.0	149.2	11.3	0.96	0.90	0.93	*10*	0	*198*
Macropus eugenii	Macropodidae	-34.4	117.9	6.5	0.85	0.83	0.84	*108*	0	*108*
Macropus fuliginosus	Macropodidae	-31.8	135.0	22.0	0.83	0.75	0.80	*10*	0	*198*
Macropus giganteus	Macropodidae	-28.5	146.3	25.9	0.92	0.91	0.92	*40*	0	*198*
Macropus irma	Macropodidae	-32.7	117.3	8.0	0.03	0.03	0.05	*40*	0	*40*
Macropus parryi	Macropodidae	-24.4	149.8	13.5	1.00	1.00	1.00	*92*	0	*92*
Macropus robustus	Macropodidae	-24.5	134.1	21.3	0.98	0.91	0.95	*130*	0	*198*
Macropus rufogriseus	Macropodidae	-31.0	149.4	16.9	0.64	0.46	0.55	*158*	0	*120*
Macropus rufus	Macropodidae	-25.4	132.9	46.3	0.87	0.85	0.86	*130*	0	*130*
Madoqua guentheri	Bovidae	4.2	41.0	7.5	0.00	0.00	0.00	*91*	0	*198*

Madoqua kirkii	Bovidae	-8.2	29.3	5.3	0.00	0.00	0.00	*26*	0	*198*
Mazama americana	Cervidae	-7.1	-61.0	22.8	0.00	0.02	0.01	*22*	0	*22*
Mazama gouazoubira	Cervidae	-20.0	-52.4	16.6	0.00	0.00	0.00	*22*	0	*22*
Mazama nemorivaga	Cervidae	-3.3	-61.4	15.0	0.02	0.02	0.02	*121*	0	*121*
Mazama rufina	Cervidae	-0.5	-77.5	26.0	0.01	0.01	0.01	*114*	0	*114*
Mazama temama	Cervidae	15.4	-88.6	18.8	0.03	0.03	0.03	*175*	0	*175*
Moschus chrysogaster	Moschidae	33.4	97.7	14.5	0.03	0.02	0.02	*69*	0	*69*
Moschus moschiferus	Moschidae	53.4	116.3	13.0	0.01	0.00	0.01	*94*	0	*94*
Muntiacus crinifrons	Cervidae	29.3	118.8	36.1	0.07	0.00	0.03	*78*	0	*78*
Muntiacus muntjak	Cervidae	0.2	108.6	15.9	0.22	0.13	0.18	*80*	0	*80*
Muntiacus reevesi	Cervidae	28.2	111.7	13.5	0.07	0.29	0.18	*59*	0	*82*
Muntiacus vuquangensis	Cervidae	14.8	107.3	36.7	0.43	0.55	0.49	*128*	0	*128*
Myocastor coypus	Myocastoridae	-34.0	-63.5	6.9	0.58	0.47	0.51	*1*	0	*1*
Naemorhedus caudatus	Bovidae	42.6	128.3	27.0	0.71	0.55	0.63	*17*	1	*30*
Naemorhedus goral	Bovidae	29.0	84.7	28.5	0.97	0.88	0.92	*80*	0	*159*
Nanger dama	Bovidae	17.4	10.1	73.0	0.64	0.49	0.56	*70, 62*	1	*70*
Nanger granti	Bovidae	-0.3	37.5	55.5	0.21	0.34	0.27	*193*	1	*20*
Nanger soemmerringii	Bovidae	11.3	41.3	40.0	0.55	0.45	0.50	*98, 47, 62*	1	*15*
Nesotragus moschatus	Bovidae	-13.1	36.2	6.5	0.00	0.00	0.00	*26*	0	*198*
Niligiritragus hylocrius	Bovidae	10.3	77.0	75.0	0.73	0.54	0.64	*163*	0	*163*
Odocoileus hemionus	Cervidae	45.1	-113.9	54.2	0.36	0.48	0.42	*103*	1	*145*
Odocoileus virginianus	Cervidae	35.3	-93.6	55.5	0.05	0.08	0.07	*11*	1	*20*
Okapia johnstoni	Giraffidae	1.3	26.5	230.0	0.00	0.00	0.00	*74*	0	*74*
Onychogalea fraenata	Macropodidae	-23.5	149.2	5.5	0.68	0.39	0.54	*10*	0	*198*
Oreamnos americanus	Bovidae	55.3	-128.3	72.5	0.11	0.27	0.21	*38*	1	*19*
Oreotragus oreotragus	Bovidae	-10.6	30.1	13.0	0.05	0.00	0.02	*83*	0	*198*
Oryx dammah	Bovidae	-12.6	17.9	200.0	0.88	0.83	0.85	*58, 62*	1	*31*
Oryx gazella	Bovidae	-24.2	20.4	169.0	0.94	0.80	0.87	*153*	1	*20*
Oryx leucoryx	Bovidae	48.6	21.1	87.7	0.92	0.88	0.90	*161, 156*	1	*62*
Ourebia ourebi	Bovidae	1.2	20.5	17.3	0.87	0.87	0.87	*26, 62*	0	*62*
Ovibos moschatus	Bovidae	73.6	-86.4	340.5	0.32	0.48	0.40	*99*	1	*31*
Ovis ammon	Bovidae	38.5	90.5	180.0	0.14	0.52	0.33	*181*	1	*31*
Ovis canadensis	Bovidae	40.9	-113.8	74.6	0.20	0.06	0.13	*122*	1	*19*
Ovis dalli	Bovidae	63.8	-139.7	55.7	0.38	0.71	0.55	*149*	1	*149*

Ovis nivicola	Bovidae	64.0	135.8	90.0	0.44	0.33	0.38	*106*	1	*17*
Ovis orientalis	Bovidae	34.3	56.2	60.0	0.28	0.09	0.16	*116*	1	*129*
Ozotoceros bezoarticus	Cervidae	-17.3	-57.1	40.0	0.20	0.17	0.18	*45*	0	*45*
Pantholops hodgsonii	Bovidae	33.6	88.3	27.5	0.28	0.59	0.44	*72, 191, 110*	1	*19*
Pecari tajacu	Tayassuidae	-4.8	-63.9	21.3	0.08	0.08	0.08	*36*	0	*198*
Pelea capreolus	Bovidae	-29.9	25.4	20.0	0.12	0.08	0.10	*124*	0	*124*
Petrogale penicillata	Macropodidae	-30.4	151.6	7.1	0.77	0.45	0.62	*10*	0	*198*
Petrogale persephone	Macropodidae	-20.4	148.5	6.2	0.60	0.49	0.54	*182*	0	*182*
Petrogale xanthopus	Macropodidae	-29.1	140.8	8.5	0.37	0.22	0.34	*42*	0	*42*
Phacochoerus africanus	Suidae	-4.6	22.2	82.5	0.91	0.91	0.91	*33*	0	*198*
Philantomba maxwellii	Bovidae	8.5	-8.1	8.6	0.00	0.00	0.00	*77*	0	*77*
Philantomba monticola	Bovidae	-4.7	23.1	6.3	0.01	0.04	0.02	*96*	0	*62*
Procapra gutturosa	Bovidae	45.9	110.0	27.8	0.40	0.60	0.50	*85*	1	*31*
Procapra picticaudata	Bovidae	34.1	91.5	20.0	0.09	0.45	0.27	*72, 191*	1	*31*
Procapra przewalskii	Bovidae	36.8	100.3	27.5	0.29	0.40	0.35	*113*	0	*198*
Pseudois nayaur	Bovidae	40.1	101.4	45.0	0.80	0.56	0.68	*126*	1	*73*
Pudu puda	Cervidae	-41.0	-72.5	9.7	0.00	0.00	0.00	*86*	0	*86*
Rangifer tarandus	Cervidae	64.2	10.9	86.0	0.51	0.28	0.40	*127*	1	*117*
Raphicerus campestris	Bovidae	-21.0	24.4	10.5	0.10	0.06	0.08	*33*	0	*198*
Raphicerus melanotis	Bovidae	-32.9	22.3	10.2	0.35	0.17	0.26	*93, 153*	0	*198*
Raphicerus sharpei	Bovidae	-14.6	31.9	9.5	0.31	0.19	0.25	*62, 151*	0	*198*
Redunca arundinum	Bovidae	-13.6	26.6	58.0	0.96	0.96	0.96	*157, 62*	0	*198*
Redunca fulvorufula	Bovidae	-15.8	31.0	29.5	0.94	0.94	0.94	*26, 62*	0	*198*
Redunca redunca	Bovidae	6.3	20.0	44.1	1.00	1.00	1.00	*26*	0	*198*
Rhinoceros unicornis	Rhinocerotidae	26.9	89.3	1602.3	0.87	0.61	0.70	*140*	0	*176*
Rucervus duvauceli	Cervidae	27.9	81.5	160.0	0.48	0.79	0.64	*167*	0	*198*
Rupicapra pyrenaica	Bovidae	42.7	0.3	30.0	0.75	0.65	0.70	*138*	1	*37*
Rupicapra rupicapra	Bovidae	44.4	22.9	26.1	0.60	0.50	0.56	*104*	1	*104, 192*
Rusa timorensis	Cervidae	-7.8	111.4	66.4	0.62	0.36	0.46	*43*	0	*198*
Rusa unicolor	Cervidae	18.6	95.3	177.5	0.63	0.46	0.54	*136*	1	*190*
Saiga tatarica	Bovidae	46.6	63.0	29.0	0.45	0.32	0.35	*18*	1	*31*
Semnopithecus entellus	Cercopithecidae	21.6	84.0	11.5	0.00	0.00	0.00	*146*	0	*146*
Sus barbatus	Suidae	0.7	110.9	70.5	0.00	0.00	0.00	*111*	0	*111*
Sylvicapra grimmia	Bovidae	-6.3	21.9	19.5	0.30	0.05	0.18	*33*	0	*198*

Syncerus caffer	Bovidae	-2.7	21.6	580.0	0.88	0.89	0.88	*33*	1	*20*
Tapirus pinchaque	Tapiridae	0.6	-77.0	148.9	0.98	0.96	0.97	*50*	1	*19*
Tapirus terrestris	Tapiridae	-8.9	-57.8	207.5	0.08	0.01	0.05	*166*	0	*198*
Taurotragus derbianus	Bovidae	8.4	17.3	680.0	0.05	0.05	0.05	*23, 75*	1	*27*
Taurotragus oryx	Bovidae	-16.2	27.4	570.0	0.05	0.00	0.03	*33*	1	*62*
Tayassu pecari	Tayassuidae	-9.0	-58.6	32.2	0.10	0.31	0.20	*44*	0	*60*
Tetracerus quadricornis	Bovidae	22.0	78.9	19.0	0.15	0.09	0.12	*102, 154*	0	*154*
Theropithecus gelada	Cercopithecidae	11.4	38.9	17.0	0.67	0.47	0.57	*56*	0	*198*
Thylogale billardierii	Macropodidae	-41.9	146.6	5.5	0.61	0.45	0.53	*158*	0	*158*
Thylogale stigmatica	Macropodidae	-22.1	148.9	5.1	0.49	0.37	0.43	*158*	0	*158*
Thylogale thetis	Macropodidae	-30.5	152.2	5.4	0.72	0.60	0.66	*158*	0	*158*
Tragelaphus angasii	Bovidae	-22.1	32.3	86.6	0.29	0.14	0.24	*33*	0	*198*
Tragelaphus eurycerus	Bovidae	3.5	14.2	329.0	0.00	0.00	0.00	*26*	0	*198*
Tragelaphus imberbis	Bovidae	2.8	40.4	81.6	0.04	0.00	0.02	*112*	0	*198*
Tragelaphus scriptus	Bovidae	-2.2	21.4	43.3	0.06	0.13	0.10	*115*	0	*198*
Tragelaphus spekii	Bovidae	-1.5	21.5	78.0	0.68	0.34	0.51	*157, 62*	0	*198*
Tragelaphus strepsiceros	Bovidae	-10.6	29.9	213.5	0.08	0.00	0.02	*135*	0	*198*
Vicugna vicugna	Camelidae	-18.4	-69.3	47.5	0.79	0.81	0.80	*171*	1	*31*
Vombatus ursinus	Vombatidae	-36.7	147.6	26.0	0.97	0.90	0.94	*55*	0	*55*
Wallabia bicolor	Macropodidae	-29.1	148.1	15.0	0.21	0.13	0.17	*79*	0	*198*

Sources:

1. Abbas, A. (1991). Feeding strategy of coypu (*Myocastor coypus*) in central western France. *Journal of Zoology*, *224*(3), 385-401.
2. Acevedo, P., & Cassinello, J. (2009). Biology, ecology and status of Iberian ibex *Capra pyrenaica*: a critical review and research prospectus. *Mammal Review*, *39*(1), 17-32.
3. Ahmad, R., Sharma, N., Mishra, C., Singh, N. J., Rawat, G. S., & Bhatnagar, Y. V. (2017). Security, size, or sociality: what makes markhor (*Capra falconeri*) sexually segregate? *Journal of Mammalogy*, *99*(1), 55-63.
4. Ahrestani, F. S., Heitkönig, I. M., & Prins, H. H. (2012). Diet and habitat-niche relationships within an assemblage of large herbivores in a seasonal tropical forest. *Journal of Tropical Ecology*, *28*(4), 385-394.
5. Akbari, H., Moradi, H. V., Rezaie, H. R., & Baghestani, N. (2016). Winter foraging of chinkara (*Gazella bennettii shikarii*) in Central Iran. *Mammalia*, *80*(2), 163-169.
6. Akram, F., Ilyas, O., & Haleem, A. (2017). Food and Feeding Habits of Indian Crested Porcupine in Pench Tiger Reserve, Madhya Pradesh, India. *Ambient Science*, *4*(1).
7. Allsopp, R., & Baldry, D. A. (1982). A general description of the Lambwe Valley area of South Nyanza District, Kenya. *Bulletin of the World Health Organization*, *47*(6), 691.

8. Andanje, S. A. (2002). Factors limiting the abundance and distribution of hirola (*Beatragus hunteri*) in Kenya.
9. Argunov, A. V., & Stepanova, V. V. (2011). Diet structure of the Siberian roe deer in Yakutia. *Russian journal of ecology*, *42*(2), 161-164.
10. Arman, S. D., & Prideaux, G. J. (2015). Dietary classification of extant kangaroos and their relatives (Marsupialia: Macropodoidea). *Austral ecology*, *40*(8), 909-922.
11. Arnold, L. A., & Drawe, D. L. (1989). Seasonal food habits of white-tailed deer in the South Texas Plains. *Journal of Range Management*, 175-178.
12. Aryal, A. (2009). Habitat ecology of himalayan serow (*Capricornis sumatraensis ssp. thar*) in Annapurna Conservation Area of Nepal. *Tiger Paper/FAO*, *36*(4), 12-20.
13. Bagchi, S., Goyal, S. P., & Sankar, K. (2003). Niche relationships of an ungulate assemblage in a dry tropical forest. *Journal of Mammalogy*, *84*(3), 981-988.
14. Baharav, D. (1980). Habitat utilization of the dorcas gazelle in a desert saline area. *Journal of Arid Environments*, *3*(2), 161-167.
15. Barker, J.R., Herlocker, D. J., & Young, S. A. (1989). Vegetal dynamics along a grazing gradient within the coastal grassland of central Somalia. *African Journal of Ecology*, *27*(4), 283-289.
16. Barrio, J. (2013). *Hippocamelus antisensis* (Artiodactyla: Cervidae). *Mammalian Species*, *45*(901), 49-59.
17. Baskin, L., & Danell, K. (2003). *Ecology of ungulates: a handbook of species in Eastern Europe and Northern and Central Asia*. Springer Science & Business Media.
18. Bekenov, A. B., Grachev, I. A., & Milner-Gulland, E. J. (1998). The ecology and management of the saiga antelope in Kazakhstan. *Mammal Review*, *28*(1), 1-52.
19. Berger, J. (2004). The last mile: how to sustain long-distance migration in mammals. *Conservation Biology*, *18*(2), 320-331.
20. Bolger, D. T., Newmark, W. D., Morrison, T. A., & Doak, D. F. (2008). The need for integrative approaches to understand and conserve migratory ungulates. *Ecology letters*, *11*(1), 63-77.
21. Bowman, D. M., Murphy, B. P., & McMahon, C. R. (2010). Using carbon isotope analysis of the diet of two introduced Australian megaherbivores to understand Pleistocene megafaunal extinctions. *Journal of Biogeography*, *37*(3), 499-505.
22. Branan, W. V., Werkhoven, M. C., & Marchinton, R. L. (1985). Food habits of brocket and white-tailed deer in Suriname. *The Journal of wildlife management*, 972-976.
23. Brandlová, K., Mallon, D., Hejcmanová, P., Regnaut, S., Jůnková Vymyslická, P., Fedorova, T., ... & Ndiaye, S. (2013). Western Derby eland (*Taurotragus derbianus derbianus*) conservation strategy. *Prague: Czech University of Life Sciences Prague*.
24. Bruno, E., & Riccardi, C. (1995). The diet of the crested porcupine *Hystrix cristata* L., 1758 in a Mediterranean rural area. *Zeitschrift für Säugetierkunde*, *60*(4), 226-236.
25. Busher, P. E. (1996). Food caching behavior of beavers (*Castor canadensis*): selection and use of woody species. *American Midland Naturalist*, 343-348.
26. Cerling, T. E., Harris, J. M., & Passey, B. H. (2003). Diets of East African Bovidae based on stable isotope analysis. *Journal of Mammalogy*, *84*(2), 456-470.
27. Chardonnet, B., & Chardonnet, P. (2004). Antelope Survey Update. Number 9: November 2004. *IUCN/SSC Antelope Specialist Group Report*.
28. Chen, H., Ma, J., Li, F., Sun, Z., Wang, H., Luo, L., & Li, F. (1998). Seasonal composition and quality of red deer *Cervus elaphus* diets in northeastern China. *Acta Theriologica*, *43*, 77-94.

29. Chetri, M. (2006). Diet analysis of gaur, *Bos gaurus gaurus* (Smith, 1827) by microhistological analysis of fecal samples in Parsa wildlife reserve, Nepal. *Our Nature*, *4*(1), 20-28.
30. Cho, C., Kim, K., & Kwon, G. (2016). Habitat altitude and home range of the endangered long-tailed goral (*Naemorhedus caudatus*): seasonal and monthly home range and altitude change. *Mammalia*, *80*(5), 481-489.
31. CMS. (2018). *Appendices I and II of the Convention on the Conservation of Migratory Species of Wild Animals (CMS).*
32. Codron, J., Lee-Thorp, J. A., Sponheimer, M., Codron, D., Grant, R. C., & de Ruiter, D. J. (2006). Elephant (*Loxodonta africana*) diets in Kruger National Park, South Africa: spatial and landscape differences. *Journal of Mammalogy*, 87(1), 27-34.
33. Codron, D., Codron, J., Lee-Thorp, J. A., Sponheimer, M., De Ruiter, D., Sealy, J., ... & Fourie, N. (2007). Diets of savanna ungulates from stable carbon isotope composition of faeces. *Journal of Zoology*, *273*(1), 21-29.
34. Codron, D., Sponheimer, M., Codron, J., Hammer, S., Tschuor, A., Braun, U., ... & Clauss, M. (2012). Tracking the fate of digesta 13C and 15N compositions along the ruminant gastrointestinal tract: Does digestion influence the relationship between diet and faeces? *European journal of wildlife research*, *58*(1), 303-313.
35. Coppedge, B. R., Leslie Jr, D. M., & Shaw, J. H. (1998). Botanical composition of bison diets on tallgrass prairie in Oklahoma. *Journal of Range Management*, 379-382.
36. Corn, J. L., & Warren, R. J. (1985). Seasonal food habits of the collared peccary in south Texas. *Journal of Mammalogy*, *66*(1), 155-159.
37. Crampe, J.P., Bon, R., Gerard, J.F., Serrano, E., Caens, P., Florence, E., and Gonzalez, G. (2007). Site fidelity, migratory behaviour, and spatial organization of female isards (*Rupicapra pyrenaica*) in the Pyrenees National Park, France. *Canadian journal of zoology 85*(1): 16-25.
38. Dailey, T. V., Hobbs, N. T., & Woodard, T. N. (1984). Experimental comparisons of diet selection by mountain goats and mountain sheep in Colorado. *The Journal of wildlife management*, 799-806.
39. Daniel, J. C., & Grubh, B. R. (1966). The Indian wild buffalo *Bubalus bubalis* (Linn.), in peninsular India: a preliminary survey. *Journal of the Bombay Natural History Society*, *63*, 32-53.
40. Dawson, T.J. (1989) Diets of macropodoid marsupials: general patterns and environmental influences. *In: Grigg, G., Jarman, P.J. & Hume, I.D. (Eds) Kangaroos, wallabies and rat-kangaroos.* New South Wales: Surrey Beatty & Sons, pp. 129-142.
41. Dawson, T. J., & Ellis, B. A. (1989). Comparison of the diets of yellow-footed rock-wallabies and sympatric herbivores in western New South Wales. *Wildlife Research*, *6*(3), 245-254.
42. Dawson, T. J., Mctavish, K. J., & Ellis, B. A. (2004). Diets and foraging behaviour of red and eastern grey kangaroos in arid shrub land: is feeding behaviour involved in the range expansion of the eastern grey kangaroo into the arid zone?. *Australian Mammalogy*, *26*(2), 169-178.
43. de Garine-Wichatitsky, M., Soubeyran, Y., Maillard, D., & Duncan, P. (2005). The diets of introduced rusa deer (*Cervus timorensis russa*) in a native sclerophyll forest and a native rainforest of New Caledonia. *New Zealand Journal of Zoology*, *32*(2), 117-126.
44. Desbiez, A. L. J., Santos, S. A., Keuroghlian, A., & Bodmer, R. E. (2009). Niche partitioning among white-lipped peccaries (*Tayassu pecari*), collared peccaries (*Pecari tajacu*), and feral pigs (*Sus scrofa*). *Journal of Mammalogy*, *90*(1), 119-128.
45. Desbiez, A. L. J., Santos, S. A., Alvarez, J. M., & Tomas, W. M. (2011). Forage use in domestic cattle (*Bos indicus*), capybara (*Hydrochoerus hydrochaeris*) and pampas deer (*Ozotoceros bezoarticus*) in a seasonal Neotropical wetland. *Mammalian Biology-Zeitschrift für Säugetierkunde*, *76*(3), 351-357.
46. Dhungel, S. K., & O'Gara, B. W. (1991). Ecology of the hog deer in Royal Chitwan National Park, Nepal. *Wildlife monographs*, 3-40.
47. Dittmann, M. T., Hebel, C., Arif, A., Kreuzer, M., & Clauss, M. (2015). Metabolic rates of three gazelle species (*Nanger soemmerringii, Gazella gazella, Gazella spekei*) adapted to arid habitats. *Mammalian Biology*, *80*(5), 390-394.

48. Djagoun, C. A. M. S., Codron, D., Sealy, J., Mensah, G. A., & Sinsin, B. (2013). Stable carbon isotope analysis of the diets of West African bovids in Pendjari Biosphere Reserve, Northern Benin. *South African Journal of Wildlife Research*, *43*(1), 33-43.
49. Doku, Y., Bekele, A., & Balakrishnan, M. (2007). Population status of plains zebra (*Equus quagga*) in Nechisar plains, Nechisar National Park, Ethiopia. *Tropical Ecology*, *48*(1), 79-86.
50. Downer, C. C. (2001). Observations on the diet and habitat of the mountain tapir (*Tapirus pinchaque*). *Journal of Zoology*, *254*(3), 279-291.
51. Dubost, G. (1984). Comparison of the diets of frugivorous forest ruminants of Gabon. *Journal of Mammalogy*, *65*(2), 298-316.
52. Ejigu, D., Bekele, A., Powell, L., & Lernould, J. M. (2015). Habitat preference of the endangered Ethiopian walia ibex (*Capra walie*) in the Simien Mountains National Park, Ethiopia. *Animal Biodiversity and Conservation*, *38*(1), 1-10.
53. Ertiban, S. M. (2016). Population status and human conflict of common hippopotamus (*Hippopotamus amphibius*, L., 1758) In Boye Wetland, Jimma, Ethiopia. *Am. J. Sci. Ind. Res., 000*, 32-40.
54. Escós, J., & Alados, C. L. (1992). Habitat preference of Spanish ibex and other ungulates in Sierras de Cazorla y Segura (Spain). *Mammalia*, *56*(3), 393-406.
55. Evans, M. C., Macgregor, C., & Jarman, P. J. (2006). Diet and feeding selectivity of common wombats. *Wildlife Research*, *33*(4), 321-330.
56. Fashing, P. J., Nguyen, N., Venkataraman, V. V., & Kerby, J. T. (2014). Gelada feeding ecology in an intact ecosystem at Guassa, Ethiopia: variability over time and implications for theropith and hominin dietary evolution. *American Journal of Physical Anthropology*, *155*(1), 1-16.
57. Fedosenko, A. K., & Blank, D. A. (2001). *Capra sibirica*. *Mammalian species*, 1-13.
58. Ferrell, S. T., Radcliffe, R. W., Marsh, R., Thurman, C. B., Cartwright, C. M., De Maar, T. W., ... & Osofsky, S. A. (2001). Comparisons among selected neonatal biomedical parameters of four species of semi-free ranging Hippotragini: Addax (*Addax nasomaculatus*), scimitar-horned oryx (*Oryx dammah*), Arabian oryx (*Oryx leucoryx*), and sable antelope (*Hippotragus niger*). *Zoo Biology: Published in affiliation with the American Zoo and Aquarium Association*, *20*(1), 47-54.
59. Forde, P. (1989). Comparative ecology of muntjac *Muntiacus reevesi* and roe deer *Capreolus capreolus* in a commercial coniferous forest. *Ph.D. Thesis. University of Bristol.*
60. Fragoso, J. M. (1998). Home Range and Movement Patterns of White-lipped Peccary (*Tayassu pecari*) Herds in the Northern Brazilian Amazon 1. *Biotropica*, *30*(3), 458-469.
61. Furstenburg, D. (2016). Sable antelope *Hippotragus niger* (Pallas, 1766). *Wildlife Biologist Scientific Report.* GeoWild Consult (Pty.) Ltd.
62. Gagnon, M., & Chew, A. E. (2000). Dietary preferences in extant African Bovidae. *Journal of Mammalogy*, 81(2), 490-511.
63. Galende, G., Ramilo, E., & Beati, A. (2005). Diet of Huemul deer (*Hippocamelus bisulcus*) in Nahuel Huapi National Park, Argentina. *Studies on Neotropical Fauna and Environment,* 40(1), 1-5.
64. García-González, R., & Cuartas, P. (1992). Feeding strategies of Spanish wild goat in the Cazorla Sierra (Spain).
65. Gazzolo, C. (2006). Botanical composition of taruka (*Hippocamelus antisensis*) diet during rainy season in Huascaran national park, Peru. In *Advances in deer biology: deer in a changing world. Proceedings of the 6th International Deer Biology Congress (L. Bartoš, A. Dušek, R. Kotrba, and J. Bartošova-Vıchova, eds.). Research Institute of Animal Production, Prague, Czech Republic* (p. 216).
66. Gebremedhin, B., Flagstad, Ø., Bekele, A., Chala, D., Bakkestuen, V., Boessenkool, S., ... & Brochmann, C. (2016). DNA metabarcoding reveals diet overlap between the endangered walia ibex and domestic goats-implications for conservation. *PloS one*, *11*(7), e0159133.
67. González, J. L., & Osbahr, K. (2013). Composición botánica y nutricional de la dieta de *Dinomys branickii* (Rodentia: Dinomyidae) en los Andes Centrales de Colombia. *Revista UDCA actualidad & divulgación científica*, *16*(1), 235-244.

68. Green, M. J. (1988). The ecology and feeding behaviour of the Himalayan tahr (*Hemitragus jemlahicus*) in the Langtang valley, Nepal (Doctoral dissertation, Durham University).
69. Green, M. J. (1987). Diet composition and quality in Himalayan musk deer based on fecal analysis. *The Journal of Wildlife Management*, 880-892.
70. Grettenberger, J. F., & Newby, J. E. (1986). The status and ecology of the dama gazelle in the Air and Tenere National Nature Reserve, Niger. *Biological Conservation*, *38*(3), 207-216.
71. Hakham, E., & Ritte, U. (1993). Foraging pressure of the Nubian ibex *Capra ibex nubiana* and its effect on the indigenous vegetation of the En Gedi Nature Reserve, Israel. *Biological conservation*, *63*(1), 9-21.
72. Harris, R. B., & Miller, D. J. (1995). Overlap in summer habitats and diets of Tibetan Plateau ungulates. *Mammalia*, *59*(2), 198-212.
73. Harris, G., Thirgood, S., Hopcraft, J. G. C., Cromsigt, J. P., & Berger, J. (2009). Global decline in aggregated migrations of large terrestrial mammals. *Endangered Species Research*, *7*(1), 55-76.
74. Hart, J. A., & Hart, T. B. (1989). Ranging and feeding behaviour of okapi (*Okapia johnstoni*) in the Ituri Forest of Zaire: food limitation in a rain-forest herbivore. In *Symposium of the Zoological Society of London* (Vol. 61, pp. 31-50).
75. Hejcmanová, P., Homolka, M., Antonínová, M., Hejcman, M., & Podhájecká, V. (2010). Diet composition of western Derby eland (*Taurotragus derbianus derbianus*) in the dry season in a natural and a managed habitat in Senegal using faecal analyses. *South African Journal of Wildlife Research*, *40*(1), 27-34.
76. Henke, S.C., Demarais, S., Pfister, J.A. (1988). Digestive capacity and diets of white-tailed deer and exotic ruminants. *J. Wildl. Manag*. 52, 595–598.
77. Hofmann, T., H. Roth. 2000. Feeding preferences of duiker (*Cephalophus maxwelli, C. rufilatus* and *C. niger*) in Ivory Coast and Ghana. *Mammalian Biology*, 68: 65-77.
78. Ho-Gee, L., & He-Lin, S. (1984). Status of the Black muntjac, *Muntiacus crinifrons*, in eastern China. *Mammal Review*, *14*(1), 29-36.
79. Hollis, C. J., Robertshaw, J. D., & Harden, R. H. (1986). Ecology of the swamp wallaby (*Wallabia bicolor*) in northeastern New-South-Wales. 1. Diet. *Wildlife Research*, *13*(3), 355-365.
80. Ilyas, O., & Khan, J. A. (2003). Food habits of barking deer (*Muntiacus muntjak*) and goral (*Naemorhedus goral*) in Binsar Wildlife Sanctuary, India. *Mammalia*, *67*(4), 521-532.
81. Iqbal, A. and B.B. Khan (2001). Feeding behaviour of Camel: A review. *Pakistan J. Agri. Sci.,* 38:3-4
82. Jackson, J. (1987). The annual diet of the Fallow deer (*Dama dama*) in the New Forest, Hampshire, as determined by rumen content analysis. *Journal of Zoology*, *181*(4), 465-473.
83. Jarman, P. J. (1981). Diets of large mammals in the woodlands around Lake Kariba, Rhodesia. *Oecologia*, *8*(2), 157-178.
84. Jhala, Y. V., & Isvaran, K. (2016). Behavioural ecology of a grassland antelope, the blackbuck *Antilope cervicapra*: linking habitat, ecology and behaviour. In *The Ecology of Large Herbivores in South and Southeast Asia* (pp. 151-176). Springer, Dordrecht.
85. Jiang, Z., Takatsuki, S., Gao, Z., & Jin, K. (1998). The present status, ecology and conservation of the Mongolian gazelle, *Procapra gutturosa*: a review. *Mammal Study*, *23*(1), 63-78.
86. Jiménez, J. E. (2010). Southern pudu *Pudu puda* (Molina 1782). *Neotropical Cervidology: Biology and Medicine of Latin American Deer. Funep & IUCN, Jaboticabal & Gland*, 140-150.
87. Joshi, R., & Singh, R. (2008). Feeding behaviour of wild Asian elephants (*Elephas maximus*) in the Rajaji National Park. *The Journal of American Science*, *4*(2), 34-48.

88. Jung, T. S., Stotyn, S. A., & Czetwertynski, S. M. (2015). Dietary overlap and potential competition in a dynamic ungulate community in northwestern Canada. *The Journal of Wildlife Management*, *79*(8), 1277-1285.
89. Jungius, H. (1988). Plan to restore Arabian oryx in Oman. *Oryx*, *14*(4), 328-336.
90. Kalule-Sabiti, M. J., & Venter, J. A. (2016). Diet composition of the large herbivores in Mkambati Nature Reserve, Eastern Cape, South Africa. *African Journal of Wildlife Research*, *46*(1), 49-56.
91. Kartzinel, T. R., Chen, P. A., Coverdale, T. C., Erickson, D. L., Kress, W. J., Kuzmina, M. L., ... & Pringle, R. M. (2015). DNA metabarcoding illuminates dietary niche partitioning by African large herbivores. *Proceedings of the National Academy of Sciences*, 201503283.
92. Kaufmann, J. H. (1984). Social ethology of the whiptail wallaby, *Macropus parryi*, in northeastern New South Wales. *Animal Behaviour*, *22*(2), 281-369.
93. Kerley, G. I., Landman, M., & De Beer, S. (2010). How do small browsers respond to resource changes? Dietary response of the Cape grysbok to clearing alien Acacias. *Functional Ecology*, *24*(3), 670-675.
94. Khadka, K. K., Singh, N., Magar, K. T., & James, D. A. (2017). Dietary composition, breadth, and overlap between seasonally sympatric Himalayan musk deer and livestock: Conservation implications. *Journal for Nature Conservation*, *38*, 30-36.
95. Khan, J. A. (1994). Food habits of ungulates in dry tropical forests of Gir Lion Sanctuary, Gujarat, India. *Acta Theriologica*, *39*(2), 185-193.
96. Kigozi, F. (2000). Feeding biology of common and blue duiker (*Doctoral dissertation, Rhodes University*).
97. Kim, B. J., Lee, N. S., & Lee, S. D. (2011). Feeding diets of the Korean water deer (*Hydropotes inermis argyropus*) based on a 202 bp rbcL sequence analysis. *Conservation Genetics*, *12*(3), 851-856.
98. Kingdon, J. (1982). *East African mammals (bovids)*. Vol. 3. P.D. Ibid.
99. Klein, D. R. (1992). Comparative ecological and behavioral adaptations of *Ovibos moschatus* and *Rangifer tarandus*. *Rangifer*, *12*(2), 47-55.
100. Kobayashi, K., & Takatsuki, S. (2012). A comparison of food habits of two sympatric ruminants of Mt. Yatsugatake, central Japan: sika deer and Japanese serow. *Acta Theriologica*, *57*(4), 343-349.
101. Krojerová-Prokešová, J., Barančeková, M., Hamšíková, L., & Vorel, A. (2010). Feeding habits of reintroduced Eurasian beaver: spatial and seasonal variation in the use of food resources. *Journal of Zoology*, *281*(3), 183-193.
102. Krishna, Y. C., Clyne, P. J., Krishnaswamy, J., & Kumar, N. S. (2009). Distributional and ecological review of the four horned antelope, *Tetracerus quadricornis*. *Mammalia*, *73*(1), 1-6.
103. Kufeld, R. C. (1983). Foods eaten by the Rocky Mountain elk. *Journal of Range Management*, 106-113.
104. La Morgia, V., & Bassano, B. (2009). Feeding habits, forage selection, and diet overlap in Alpine chamois (*Rupicapra rupicapra* L.) and domestic sheep. *Ecological Research*, *24*(5), 1043-1050.
105. Lamprey, H. (1963). Ecological separation of the large mammal species in the Tarangire Game Reserve, Tanaganyika. *East African Wildlife Journal*, *1*, 63-93.
106. Larin, VV, Shelkonivoka, TA (1988). Season peculiarities of the feeding ecology of *Ovis nivicola* in the Delochi river basin. 17-26.
107. Larter, N. C., & Gates, C. C. (1991). Diet and habitat selection of wood bison in relation to seasonal changes in forage quantity and quality. *Canadian Journal of Zoology*, *69*(10), 2677-2685.
108. Lentle, R. G., Potter, M. A., Stafford, K. J., Springett, B. P., & Haslett, S. (1998). The temporal characteristics of feeding activity in free-ranging tammar wallabies (*Macropus eugenii* Desmarest). *Australian Journal of Zoology*, *46*(6), 601-615.
109. Leslie, D. M., Lee, D. N., & Dolman, R. W. (2013). *Elaphodus cephalophus* (Artiodactyla: Cervidae). *Mammalian Species*, *45*(904), 80-91.

110. Leslie, D. M., & Schaller, G. B. (2008). *Pantholops hodgsonii* (Artiodactyla: Bovidae). *Mammalian Species*, (817), 1-13.
111. Leus, K., & Macdonald, A. A. (1997). From babirusa (*Babyrousa babyrussa*) to domestic pig: the nutrition of swine. *Proceedings of the Nutrition Society*, *56*(3), 1001-1012.
112. Leuthold, W. (1981). Studies on the food habits of lesser kudu in Tsavo National Park, Kenya. *African Journal of Ecology*, *9*(1), 35-45.
113. Li, Z., Jiang, Z., & Li, C. (2008). Dietary Overlap of Przewalski's Gazelle, Tibetan Gazelle, and Tibetan Sheep on the Qinghai-Tibet Plateau. *The Journal of Wildlife Management*, *72*(4), 944-948.
114. Lizcano, D. J. (2006). *Ecology and conservation of large mammals in the northern Andes.* Ph.D., University of Kent, Canterbury.
115. MacLeod, S. B., Gaylard, A., & Kerley, G. I. H. (1996). Habitat and diet of bushbuck *Tragelaphus scriptus* in the Woody Cape Nature Reserve: observations from faecal analysis. *South African Journal of Wildlife Research-24-month delayed open access*, *26*(1), 19-25.
116. Maisels, F.G. (1988). The feeding ecology of the Cyprus mouflon *Ovis orientalis* Gmelin 1774, the the Paphos Forest, Cyprus.
117. Mager K.H., Colson K.E., Groves P., Hundertmark K.J. (2014). Population structure over a broad spatial scale driven by nonanthropogenic factors in a wide-ranging migratory mammal, Alaskan caribou. *Mol Ecol,* 23, 6045-6057.
118. Mayer, J. J., & Wetzel, R. M. (1986). *Catagonus wagneri*. *Mammalian Species*, (259), 1-5.
119. McCarthy, T.S., Ellery, W.N. and Bloem, A., 1998. Some observations on the geomorphological impact of hippopotamus (*Hippopotamus amphibius* L.) in the Okavango Delta, Botswana. *African Journal of Ecology*, *36*(1), pp.44-56.
120. McCullough DR, McCullough Y (2000) Kangaroos in outback Australia: comparative ecology and behaviour of three coexisting species. Columbia University Press, New York.
121. Merino, M. L., & Rossi, R. V. (2010). Origin, systematics and morphological radiation. *Neotropical Cervidology. Biology and medicine of Latin American deer*, *1*, 2-11.
122. Miller, G. D., & Gaud, W. S. (1989). Composition and variability of desert bighorn sheep diets. *The Journal of Wildlife Management*, 597-606.
123. Miller, D. J., Harris, R. B., & Cai, G. Q. (1994). Wild yaks and their conservation on the Tibetan Plateau. In *Proceedings of the First International Congress on Yak* (27-35). Gansu Agricultural University Lanzhou.
124. Mills, G., & Hes, L. (1997). The Mammals of Southern Africa.
125. Mimoun, J. B., & Nouira, S. (2015). Food habits of the aoudad *Ammotragus lervia* in the Bou Hedma mountains, Tunisia. *South African Journal of Science*, *111*(11-12), 1-5.
126. Mishra, C., Van Wieren, S. E., Ketner, P., Heitkönig, I. M., & Prins, H. H. (2004). Competition between domestic livestock and wild bharal *Pseudois nayaur* in the Indian Trans-Himalaya. *Journal of Applied Ecology*, *41*(2), 344-354.
127. Mysterud, A. (2000). Diet overlap among ruminants in Fennoscandia. *Oecologia 124*(1): 130-7.
128. Nagarkoti, A., & Thapa, T. (2007). Food habits of barking deer (Muntiacus muntjac) in the middle hills of Nepal. *Hystrix, the Italian Journal of Mammalogy*, *18*(1).
129. Najafabadi, S.M., Hemami, M.R., Salman Mahini, A. (2010). Determining habitat suitability of *Ovis orientalis isfahanica* in Mothe Wildlife Refuge using ENFA. *J. Nat. Environ. (Iran. J. Nat. Resour.)* 63: 279-290.
130. Newsome, A. E. (1985). An ecological comparison of the two arid-zone kangaroos of Australia, and their anomalous prosperity since the introduction of ruminant stock to their environment. *The Quarterly Review of Biology*, *50*(4), 389-424.
131. Nie, Y., Zhang, Z., Raubenheimer, D., Elser, J. J., Wei, W., & Wei, F. (2015). Obligate herbivory in an ancestrally carnivorous lineage: the giant panda and bamboo from the perspective of nutritional geometry. *Functional Ecology*, *29*(1), 26-34.

132. Nunez, T. (2017). *Animal movement in a changing world.* Doctoral dissertation, UC Berkeley.

133. Ochiai, K. (1999). Diet of the Japanese serow (*Capricornis crispus*) on the Shimokita Peninsula, northern Japan, in reference to variations with a 16-year interval. *Mammal Study*, *24*(2), 91-102.

134. O'shaughnessy, R., Cain III, J., & Owen-Smith, N. (2014). Comparative diet and habitat selection of puku and lechwe in northern Botswana. *J. Mammalogy 95*(5): 933-942.

135. Owen-Smith, N., Cooper, S. (1989). Nutritional ecology of a browsing ruminant, the kudu (*Tragelaphus strepsiceros*), through the seasonal cycle. *J. Zoology 219*(1): 29-43.

136. Padmalal, U., Takatsuki, S., & Jayasekara, P. (2003). Food habits of sambar *Cervus unicolor* at the Horton Plains National Park, Sri Lanka. *Ecological Research*, *18*(6): 775-782.

137. Parrini, F., Cain, J. W., & Krausman, P. R. (2009). *Capra ibex* (Artiodactyla: Bovidae). *Mammalian Species*, (830), 1-12.

138. Perez-Barberia, F.J., Olivan, M., Osoro, K., and Nores, C. (1997). Sex, seasonal and spatial differences in the diet of Cantabrian chamois Rupicapra pyrenaica parva. *Acta Theriologica* 42: 37-46.

139. Perzanowski, K., Januszczak, M., & Wołoszyn-Gałęza, A. (2012). Seasonal movements of wisents (*Bison bonasus* L., 1758) in the Bieszczady Mountains (SE Poland). *Biological Letters*, *49*(1), 11-17.

140. Pradhan, N., Wegge, P., Moe, S., & Shrestha, A. (2008). Feeding ecology of two endangered sympatric megaherbivores: Asian elephant *Elephas maximus* and greater one-horned rhinoceros *Rhinoceros unicornis* in lowland Nepal. *Wildlife Biology*, *14*(1), 147-154.

141. Puig, S., Videla, F., Monge, S., & Roig, V. (1996). Seasonal variations in guanaco diet (*Lama guanicoe* Müller 1776) and food availability in Northern Patagonia, Argentina. *Journal of Arid Environments*, *34*(2), 215-224.

142. Pujaningsih, R. I., Sutrisno, C. I., Supriondho, Y., Malik, A., Djuwantoko, D., Pudyatmoko, S., ... & Aryanto, S. (2009). Diet composition of Anoa (*Bubalus* sp.) studied using direct observation and dung analysis method in their habitat. *Journal of the Indonesian Tropical Animal Agriculture*, *34*(3), 223-228.

143. Raedeke, K. J. (1980). Food habits of the guanaco (*Lama guanicoe*) of Tierra de Fuego, Chile. *Turrialba*, *30*(2), 177-181.

144. Reilly, J., & Spedding, G. H. (1997). Preliminary observations on the Sumatran rhino in Way Kambas National Park, Indonesia. *Oryx*, *31*(2), 143-150.

145. Sawyer, H., F. Lindzey, and D. McWhirter. 2005. Mule deer and pronghorn migration in western Wyoming. *Wildlife Society Bulletin* 33:1266–1273.

146. Sayers, K., & Norconk, M. A. (2008). Himalayan *Semnopithecus entellus* at Langtang National Park, Nepal: diet, activity patterns, and resources. *International Journal of Primatology*, *29*(2), 509.

147. Schaller, G.B., Qitao, T., Wenshi, P., Zisheng, Q., Xiaoming, W., Jinchu, H., & Heming, S. (1986). Feeding behavior of Sichuan takin (*Budorcas taxicolor*). *Mammalia*, *50*(3), 311-322.

148. Schulz, E., Fraas, S., Kaiser, T. M., Cunningham, P. L., Ismail, K., & Wronski, T. (2013). Food preferences and tooth wear in the sand gazelle (*Gazella marica*). *Mammalian Biology-Zeitschrift für Säugetierkunde*, *78*(1), 55-62.

149. Seip, D.R. 1983. *Foraging ecology and nutrition of Stone's sheep.* Ph.D. Thesis, Univ. British Columbia, Vancouver.

150. Skinner, G. N. (1996). The Springbok: *Antidorcas marsupialis* (Zimmermann, 1790). Ecology and physiology. Behaviour. *Transvaal Museum Monographs*, *10*(1).

151. Skinner, J. D., & Smithers, R. H. (1990). *The Mammals of the Southern African Subregion. University of Pretoria, South Africa.*

152. Smith, M. (1991) *Faecal Composition as Indicator of Diet Composition in the Cape Grysbok,* Raphicerus melanotis. Honors thesis, University of Port Elizabeth, South Africa
153. Smith, C., Valdez, R., Holechek, J. L., Zwank, P. J., & Cardenas, M. (1998). Diets of native and non-native ungulates in southcentral New Mexico. *The Southwestern Naturalist*, 163-169.
154. Solanki, G. S., & Naik, R. M. (1998). Grazing interactions between wild and domestic herbivores. *Small Ruminant Research*, *27*(3), 231-235.
155. Sombra, M. S., & Mangione, A. M. (2005). ¿Obsesionada con gramíneas?: el caso de Mara *Dolichotis patagonum* (Caviidae: Rodentia). *Revista chilena de historia natural*, *78*(3), 393-399.
156. Spalton, J. A. (1999). The food supply of Arabian oryx (*Oryx leucoryx*) in the desert of Oman. *Journal of Zoology*, *248*(4), 433-441.
157. Sponheimer, M., Robinson, T., Ayliffe, L., Passey, B., Roeder, B., Shipley, L., ... & Ehleringer, J. (2003). An experimental study of carbon-isotope fractionation between diet, hair, and feces of mammalian herbivores. *Canadian Journal of Zoology*, *81*(5), 871-876.
158. Sprent, J. A., & McArthur, C. (2002). Diet and diet selection of two species in the macropodid browser–grazer continuum—do they eat what they 'should'? *Australian Journal of Zoology*, *50*(2), 183-198.
159. Srivastava, T., & Kumar, A. (2018). Seasonal habitat use in three species of wild ungulates in Sikkim Himalaya. *Mammalian Biology*, *88*, 100-106.
160. Stephenson, T. E., Holecheck, J. L., & Kuykendall, C. B. (1985). Drought effect on pronghorn and other ungulate diets. *The Journal of wildlife management*, *49*(1), 146-151.
161. Stewart, D. R. M. (1963). The Arabian oryx (*Oryx leucoryx* Pallas). *African Journal of Ecology*, *1*(1), 103-117.
162. Stone, J. L. (1981). Winter movements and distribution of moose (*Alces alces shirasi*) in Upper Rock Creek drainage Granite County Montana.
163. Sumithran, S. (1997). *Status and ecology of the Nilgiri Tahr in the Mukurthi National Park, South India* (Doctoral dissertation, Virginia Tech).
164. Takatsuki, S., Ohtaishi, N., Kaji, K., Han, Y., & Wu, J. (1988). A note on fecal and rumen contents of white-lipped deer on eastern Qinghai-Tibet Plateau. *Journal of the Mammalogical Society of Japan*, *13*(2), 133-137.
165. Takatsuki, S., Fuse, S., & Ito, T. (2010). A comparison of diet and digestion between sika deer and Japanese serow in northern Japan. *Mammal study*, *35*(4), 257-263.
166. Talamoni, S. A., & Cançado, M. A. (2009). Feeding habit of the Brazilian tapir, *Tapirus terrestris* (Perissodactyla: Tapiridae) in a vegetation transition zone in south-eastern Brazil. *Zoologia*, *26*(2).
167. Tewari, R., & Rawat, G. S. (2013). Habitat use of Swamp Deer (*Rucervus duvaucelii duvaucelii*) in Jhilmil Jheel Conservation Reserve, Haridwar, Uttarakhand, India. *International Journal of Ecology and Conservation Science*, *39*, 79-85.
168. Thirgood, S. J. (1995). The effects of sex, season and habitat availability on patterns of habitat use by fallow deer (*Dama dama*). *Journal of Zoology*, *235*(4), 645-659.
169. Tinley, K. L. (1987). *Framework of the Gorongosa Ecosystem, Mozambique.* PhD thesis, Univ. Pretoria.
170. Tomas, W. M., & Salis, S. M. (2000). Diet of the marsh deer (*Blastocerus dichotomus*) in the Pantanal wetland, Brazil. *Studies on Neotropical Fauna & Environment*, *35*(3), 165-172.
171. Torres, M., & Puig, S. (2010). Seasonal diet of vicuñas in the Los Andes protected area (Salta, Argentina): Are they optimal foragers? *Journal of Arid Environments*, *74*(4), 450-457.

172. Trisurat, Y. (2006). Transboundary biodiversity conservation of the Pha Taem Protected Forest Complex: A bioregional approach. *Applied Geography*, 26(3-4): 260-275.
173. Tulloch, D. (1980). Season movement and distribution of the sexes in the water buffalo, *Bubalus bubalis*, in the Northern Territory. *Australian Journal of Zoology 18*(4): 399-414.
174. Viljoen, P.C. 1980. Distribution and numbers of the hippopotamus in the Olifants and Blyde Rivers. *S. Afr. J. Wildl. Res.* 10: 129–132.
175. Villarreal-Espino-Barros, O. A., Campos-Armendia, L. E., Castillo-Martínez, T. A., Cortes-Mena, I., Plata-Pérez, F. X., & Mendoza-Martínez, G. D. (2008). Composición botánica de la dieta del venado temazate rojo (*Mazama temama*), en la sierra nororiental del estado de Puebla. *Universidad y ciencia*, *24*(3), 183-188.
176. Walker, E.P., Warnick, F., Lange, K.I., Uible, H.E., Hamlet, S.E., Davies, M.A. & Wright P. F. (1968). *Mammals of the World*. The John Hopkins Press, Baltimore, vol. 1, 2: 1-1500.
177. Wang, T., Skidmore, A. K., Zeng, Z., Beck, P. S., Si, Y., Song, Y., ... & Prins, H. H. (2010). Migration patterns of two endangered sympatric species from a remote sensing perspective. *Photogrammetric Engineering & Remote Sensing*, *76*(12), 1343-1352.
178. Wegge, P., Shrestha, A. K., & Moe, S. R. (2006). Dry season diets of sympatric ungulates in lowland Nepal: competition and facilitation in alluvial tall grasslands. *Ecological Research*, *21*(5), 698-706.
179. Weinberg, P. J. (2002). *Capra cylindricornis*. *Mammalian Species*, 1-9.
180. Wharton, C. H. 1957. *An ecological study of the Kouprey* Novibos sauveli (*Urbain*). Manila: Institute of Science and Technology (monograph 5).
181. Wingard, G. J., Harris, R. B., Pletscher, D. H., Bedunah, D. J., Mandakh, B., Amgalanbaatar, S., & Reading, R. P. (2011). Argali food habits and dietary overlap with domestic livestock in Ikh Nart Nature Reserve, Mongolia. *Journal of Arid Environments*, 75(2), 138-145.
182. Winkel, P. (1997). *The ecology and management of the Proserpine rock-wallaby (*Petrogale persephone*)*.
183. Winkler A 1992. *The Feeding Ecology of the Cape Mountain Zebra (*Equus zebra zebra *Linn., 1758) in the Mountain Zebra National Park, South Africa.* MSc Thesis, University of Witwatersrand, Johannesburg, South Africa.
184. Woodman, H. M. (1965). What of Sudan Game Migration? *Oryx*, *8*(2), 113-114.
185. Woolnough, A. P. (1998). *The feeding ecology of the northern hairy-nosed wombat,* Lasiorhinus krefftii *(Marsupialia: Vombatidae)* (Doctoral dissertation, James Cook University).
186. Wronski, T., & Schulz-Kornas, E. (2015). The Farasan gazelle—A frugivorous browser in an arid environment? *Mammalian Biology-Zeitschrift für Säugetierkunde*, *80*(2), 87-95.
187. Xu, W., Xia, C., Lin, J., Yang, W., Blank, D. A., Qiao, J., & Liu, W. (2012). Diet of *Gazella subgutturosa* (Güldenstaedt, 1780) and food overlap with domestic sheep in Xinjiang, China. *Folia Zoologica*, *61*(1), 54-61.
188. Xu, W., Xia, C., Yang, W., Blank, D. A., Qiao, J., & Liu, W. (2012). Seasonal diet of khulan (Equidae) in northern Xinjiang, China. *Italian Journal of Zoology*, *79*(1), 92-99.
189. Yockney, I. J., & Hickling, G. J. (2000). Distribution and diet of chamois (*Rupicapra rupicapra*) in Westland forests, South Island, New Zealand. *New Zealand Journal of Ecology*, 31-38.
190. Yen, S. C., Wang, Y., Yu, P. H., Kuan, Y. P., Liao, Y. C., Chen, K. H., & Weng, G. J. (2019). Seasonal space use and habitat selection of sambar in Taiwan. *The Journal of Wildlife Management*, *83*(1), 22-31.
191. Yin, B. F., Huai, H. Y., Zhang, Y. L., Le, Z., & Wei, W. H. (2007). Trophic niches of *Pantholops hodgsoni, Procapra picticaudata* and *Equus kiang* in Kekexili region. *The Journal of Applied Ecology*, *18*(4), 766-770.

192. Fryxell, J. M., & Sinclair, A. R. E. (1988). Causes and consequences of migration by large herbivores. *Trends in ecology & evolution*, *3*(9), 237-241.
193. Hansen, R. M., Mugambi, M. M., & Bauni, S. M. (1985). Diets and trophic ranking of ungulates of the northern Serengeti. *The Journal of wildlife management*, 823-829.
194. Cerling, T. E., Wittemyer, G., Rasmussen, H. B., Vollrath, F., Cerling, C. E., Robinson, T. J., & Douglas-Hamilton, I. (2006). Stable isotopes in elephant hair document migration patterns and diet changes. *Proceedings of the National Academy of Sciences*, *103*(2), 371-373.
195. Cerling, T. E., & Viehl, K. (2004). Seasonal diet changes of the forest hog (Hylochoerus meinertzhageni Thomas) based on the carbon isotopic composition of hair. *African Journal of Ecology*, *42*(2), 88-92.
196. Keast, A. (1965). Interrelationships of two zebra species in an overlap zone. *Journal of Mammalogy*, *46*(1), 53-66.
197. Gaidet, N., & Lecomte, P. (2013). Benefits of migration in a partially-migratory tropical ungulate. *BMC ecology*, *13*(1), 1-14.
198. No record of migration available in Web of Science or Google Scholar.

Table S2. Variable abbreviations used in model selection along with their corresponding definitions and the ecological interpretation of each variable

Variable name	Variable definition	Ecological interpretation
logBM	log-transformed body mass	Herbivore body masses vary by orders of magnitude (from 5 kg to nearly 4,000 kg). This variable corresponds to the order of magnitude of herbivore body mass.
$(\text{logBM})^2$	polynomial transformation of log-transformed body mass	The second-order polynomial transformation of log-transformed herbivore body mass. This transformation was done to test whether herbivores of intermediate body size are most able to migrate and/or shift their diets.
avg_grass_diet	average dietary grass fraction	An herbivore's average grass dependence, quantified as the average grass fraction in its diet across seasons.
$(\text{avg\_grass\_diet})^2$	polynomial transformation of average dietary grass fraction	The second-order polynomial transformation of an herbivore's average grass dependence (quantified as the average grass fraction in its diet across seasons). This transformation was done to test whether herbivores with intermediate dietary preferences have the largest home ranges.
grow_grass_diet	growing season dietary grass fraction	An herbivore's growing season grass dependence, quantified as the average grass fraction in its diet during the summer/wet season.
dorm_grass_diet	dormant season dietary grass fraction	An herbivore's dormant season grass dependence, quantified as the average grass fraction in its diet during the winter/dry season.
$(\text{grow\_grass\_diet})^2$	polynomial transformation of growing season dietary grass fraction	The second-order polynomial transformation of an herbivore's growing season grass dependence (quantified as the average grass fraction in its diet during the summer/wet season). This transformation was done to test whether herbivores with intermediate dietary preferences are most able to shift their diets.
migration	seasonal migration	Whether or not an herbivore species is migratory. Coded as a binary (1 = migratory, 0 = non-migratory).
diet_shift	seasonal dietary shifts	The magnitude of seasonal dietary shifts. Quantified as the change in dietary grass fraction between the growing and dormant season.
abs(latitude)	absolute value of latitude	The absolute value of the latitudinal centroid of an herbivore's species range. Corresponds to average distance from the equator for each herbivore species.
mean_temp_mean	mean annual temperature	Mean annual temperature averaged across an herbivore's species range. As such, corresponds to the average temperatures experienced by the species.

mean_temp_sd	standard deviation of mean annual temperature	The standard deviation of mean annual temperature across an herbivore's species range. As such, corresponds to spatial variability in temperature.
temp_seas_mean	mean temperature seasonality	Temperature seasonality averaged across an herbivore's species range. As such, corresponds to the average temperature seasonality experienced by the species.
temp_seas_sd	standard deviation of temperature seasonality	The standard deviation of temperature seasonality across an herbivore's species range. As such, corresponds to spatial variability in temperature seasonality.
annu_rain_mean	annual rainfall	Annual rainfall averaged across an herbivore's species range. As such, corresponds to the average rainfall experienced by the species.
annu_rain_sd	standard deviation of annual rainfall	The standard deviation of annual rainfall averaged across an herbivore's species range. As such, corresponds to spatial variability in rainfall.
rain_seas_mean	mean rainfall seasonality	Mean rainfall seasonality averaged across an herbivore's species range. As such, corresponds to the average rainfall seasonality experienced by the species.
rain_seas_sd	standard deviation of rainfall seasonality	The standard deviation of rainfall seasonality across an herbivore's species range. As such, corresponds to spatial variability in rainfall seasonality.
cec_mean	mean effective cation exchange capacity of soil	Average effective cation exchange capacity of all soil data points within an herbivore's species range. Higher values reflect comparatively nutrient rich soils.
cec_sd	standard deviation of effective cation exchange capacity of soil	The standard deviation of effective cation exchange capacity for all soil data points within an herbivore's species range. Higher values reflect more spatially variable soil nutrients.
nit_mean	mean nitrogen content of soil	Average nitrogen content of all soil data points within an herbivore's species range. Higher values reflect comparatively nutrient rich soils.
nit_sd	standard deviation of mean nitrogen content of soil	The standard deviation of nitrogen content for all soil data points within an herbivore's species range. Higher values reflect more spatially variable soil nutrients.

Table S3. Global models of herbivore traits and behaviors, including all predictors hypothesized that have an effect on said variable, for use in model selection. Note that predictors that are underlined were only included in the analyses involving soil nutrient data, which encompass only the subset of species for which nutrient data were available.

Variable	Global model
body mass	logBM ~ abs(latitude) + mean_temp_mean + mean_temp_sd + temp_seas_mean +annu_rain_mean*[nit_mean + nit_sd + cec_mean + cec_sd]
grass dependence	avg_grass_diet ~ logBM * abs(latitude)+ temp_seas_mean + rain_seas_mean + annu_rain_mean*[nit_mean + nit_sd + cec_mean + cec_sd]
migration	migration ~ (logBM)^2 + grow_grass_diet + diet_shift*[abs(latitude) + rain_seas_mean + annu_rain_sd + temp_seas_mean + mean_temp_sd] + annu_rain_mean*[nit_mean + nit_sd + cec_mean + cec_sd]
dietary shifts	diet_shift ~ (logBM)^2 + (grow_grass_diet)^2+ migration*[abs(latitude) + rain_seas_mean + annu_rain_sd + temp_seas_mean + mean_temp_sd] + annu_rain_mean*[nit_mean + nit_sd + cec_mean + cec_sd]

Table S4. Model selection results for the predictors of herbivore body mass using different data subsets. Only the 6-8 highest ranked models are listed. 'Preferred' models (all models with $\Delta AIC_c < 2$) are *italicized*, whereas the 'best' model (simplest model with $\Delta AIC_c < 2$) is **bolded**.

Data set	Model formula	R^2	K	logLik	AICc	ΔAICc	weight
All herbivores with nutrient data (*N* = 158)	***Intercept only***	**0.0356**	**2**	**-148.6**	**301.3**	**0**	**0.829**
	logBM~mean_temp_sd	0.0525	3	-149.8	305.8	4.507	0.087
	logBM~nit_mean	0.0356	3	-150.8	307.7	6.404	0.034
	logBM~nit_sd	0.0358	3	-151.4	309.0	7.644	0.018
	logBM~cec_sd	0.0386	3	-152.4	310.9	9.566	0.007
	logBM~cec_mean	0.0409	3	-152.5	311.1	9.775	0.006
	logBM~mean_temp_mean	0.0356	3	-152.9	311.9	10.615	0.004
	logBM ~mean_temp_sd+nit_mean	0.0528	4	-152.0	312.2	10.875	0.004
All herbivores (*N* = 210)	***Intercept only***	**0.0539**	**2**	**-191.3**	**386.7**	**0**	**0.937**
	logBM~mean_temp_sd	0.0626	3	-193.1	392.4	5.681	0.055
	logBM~mean_temp_mean	0.0552	3	-195.6	397.4	10.728	0.004
	logBM~abs(latitude)	0.0558	3	-196.1	398.4	11.712	0.003
	logBM~mean_temp_mean + mean_temp_sd	0.0687	4	-197.4	403.0	16.367	0
	logBM~mean_temp_mean + mean_temp_sd	0.0626	4	-197.5	403.2	16.545	0
Herbivores < 500 kg	***Intercept only***	**0.0657**	**2**	**-130.1**	**264.2**	**0**	**0.939**
	logBM~mean_temp_sd	0.0728	3	-132.3	270.8	6.571	0.035
	logBM~mean_temp_mean	0.0851	3	-132.8	271.7	7.452	0.023
	logBM~abs(latitude)	0.067	3	-135.2	276.5	12.244	0.002
	logBM~mean_temp_mean + mean_temp_sd	0.0859	4	-135.6	279.4	15.144	0
	logBM~abs(latitude) + mean_temp_mean	0.0996	4	-136.0	280.2	15.987	0
Herbivores 50 - 500 kg (*N* = 81)	***Intercept only***	**0.0608**	**2**	**-12.23**	**28.62**	**0**	**0.98**
	logBM~mean_temp_sd	0.0609	3	-15.34	36.99	8.372	0.015
	logBM~mean_temp_mean	0.0658	3	-16.96	40.22	11.601	0.003
	logBM~abs(latitude)	0.0608	3	-17.69	41.7	13.075	0.001
	logBM~temp_seas_mean	0.0652	3	-20.53	47.38	18.753	0
	logBM~annu_rainfall_mean	0.0708	3	-20.84	48	19.377	0
	logBM~mean_temp_mean + mean_temp_sd	0.0673	4	-19.92	48.38	19.753	0
Ungulates only (*N* =175)	***Intercept only***	**0.0686**	**2**	**-146.3**	**296.7**	**0**	**0.918**
	logBM~mean_temp_sd	0.0821	3	-147.8	301.7	5.048	0.074
	logBM~mean_temp_mean	0.0714	3	-150.6	307.2	10.585	0.005
	logBM~abs(latitude)	0.0710	3	-151.1	308.4	11.730	0.003
	logBM~mean_temp_mean + mean_temp_sd	0.0821	4	-152.2	312.6	15.989	0
	logBM~abs(latitude) + mean_temp_sd	0.0822	4	-152.8	313.8	17.117	0

Table S5. Model selection results for the predictors of herbivore grass dependence (defined here as mean dietary grass fraction) using different data subsets. Only the 6-8 highest ranked models are listed. 'Preferred' models (all models with $\Delta AIC_c < 2$) are *italicized*, whereas the 'best' model (simplest model with $\Delta AIC_c < 2$) is **bolded**.

Data set	Model formula	R^2	K	logLik	AICc	ΔAICc	weight
All herbivores with nutrient data (*N* = 158)	***avg_grass_diet~logBM***	**0.1143**	**3**	**-61.3**	**128.7**	**0**	**0.71**
	avg_grass_diet~logBM+nit_mean	0.1334	4	-62.3	132.9	4.191	0.087
	avg_grass_diet~logBM+nit_sd	0.1382	4	-62.5	133.3	4.592	0.071
	avg_grass_diet~logBM+cec_sd	0.1446	4	-63.1	134.5	5.817	0.039
	avg_grass_diet~logBM+cec_mean	0.1466	4	-63.2	134.7	6.023	0.035
	Intercept only	0.0329	2	-66	136.1	7.372	0.018
	avg_grass_diet~logBM+annu_rain_mean	0.1758	4	-64.7	137.7	8.975	0.008
	avg_grass_diet~logBM+rain_seas_mean	0.1369	4	-65.2	138.6	9.885	0.005
All herbivores (*N* = 210)	***avg_grass_diet~logBM***	**0.0882**	**3**	**-76.02**	**158.2**	**0**	**0.921**
	Intercept only	0.0324	2	-79.92	163.9	5.733	0.052
	avg_grass_diet~logBM+annu_rain_mean	0.1386	4	-79.38	167.0	8.809	0.011
	avg_grass_diet~logBM+rain_seas_mean	0.1114	4	-79.49	167.2	9.028	0.01
	avg_grass_diet~ rain_seas_mean	0.0713	3	-81.79	169.7	11.533	0.003
	avg_grass_diet~logBM +abs(latitude)	0.0920	4	-81.18	170.6	12.403	0.002
Herbivores < 500 kg (*N* = 192)	***avg_grass_diet~logBM***	**0.1293**	**3**	**-64.59**	**135.3**	**0**	**0.964**
	avg_grass_diet~logBM+annu_rain_mean	0.1873	4	-67.29	142.8	7.485	0.023
	avg_grass_diet~logBM+rain_seas_mean	0.1534	4	-68.07	144.4	9.059	0.01
	avg_grass_diet~logBM +abs(latitude)	0.1315	4	-69.91	148.0	12.742	0.002
	Intercept only	0.0272	2	-73.11	150.3	14.990	0.001
	avg_grass_diet~logBM*abs(latitude)	0.1589	5	-71.78	153.9	18.577	0
	avg_grass_diet~logBM+abs(latitude)+ annu_rain_mean	0.1928	5	-72.12	154.6	19.272	0
Herbivores 50 - 500 kg (*N* = 81)	***Intercept only***	**0.0160**	**2**	**-33.11**	**70.37**	**0**	**0.431**
	avg_grass_diet~logBM	0.0541	3	-32.56	71.43	1.056	0.254
	avg_grass_diet~rain_seas_mean	0.1596	3	-32.60	71.51	1.136	0.244
	avg_grass_diet~logBM+rain_seas_mean	0.1789	4	-32.76	74.05	3.673	0.069
	avg_grass_diet~abs(latitude)	0.0210	3	-38.11	82.53	12.159	0.001
	avg_grass_diet~logBM +abs(latitude)	0.0589	4	-37.58	83.68	13.305	0.001
	avg_grass_diet~ rain_seas_mean +abs(latitude)	0.1600	4	-37.82	84.17	13.794	0
Ungulates only (*N*=175)	***avg_grass_diet~logBM***	**0.1718**	**3**	**-54.74**	**115.6**	**0**	**0.621**
	avg_grass_diet~ logBM+rain_seas_mean	0.2334	4	-54.19	116.6	0.999	0.377
	avg_grass_diet~logBM+annu_rain_mean	0.2086	4	-60.08	128.4	12.776	0.001
	avg_grass_diet~logBM +abs(latitude)	0.1725	4	-60.27	128.8	13.14	0.001
	avg_grass_diet~ logBM+rain_seas_mean +abs(latitude)	0.2380	5	-59.28	128.9	13.295	0.001
	avg_grass_diet~ logBM + annu_rain_mean + rain_seas_mean	0.2447	5	-62.13	134.6	18.983	0

Table S6. Model selection results for the predictors of migration using different data subsets. Only the 5-7 highest ranked models are listed. 'Preferred' models (all models with $\Delta AIC_c < 2$) are *italicized*, whereas the 'best' model (simplest model with $\Delta AIC_c < 2$) is **bolded**.

Data set	Model formula	R^2	K	logLik	AICc	ΔAICc	weight
All herbivores with nutrient data (*N* = 158)	*migration~ (logBM)^2+ abs(latitude)*	0.430	5	-76.50	163.39	0	0.109
	migration~ (logBM)^2+ diet_shift	0.389	5	-76.84	164.08	0.694	0.077
	migration~ (logBM)^2+ grow_grass_diet + abs(latitude)	0.446	6	-75.83	164.22	0.828	0.072
	migration~ (logBM)^2+ grow_grass_diet + diet_shift	0.405	6	-76.29	165.14	1.749	0.045
	migration~ (logBM)^2+ abs(latitude)+ diet_shift	0.434	6	-76.32	165.19	1.798	0.044
	migration~(logBM)^2	**0.373**	**4**	**-78.48**	**165.23**	**1.835**	**0.043**
	migration~ logBM + grow_grass_diet + abs(latitude)	0.420	5	-77.54	165.47	2.078	0.038
	migration~ logBM + abs(latitude)	0.400	4	-78.62	165.49	2.102	0.038
All herbivores (*N* = 210)	*migration~abs(latitude)+(logBM)^2 + grow_grass_diet*	0.447	6	-101.3	215.0	0	0.363
	migration~abs(latitude)+logBM+ grow_grass_diet + diet_shift	0.452	7	-100.8	216.1	1.098	0.210
	migration~abs(latitude)+logBM + grow_grass_diet	**0.425**	**5**	**-103.3**	**216.9**	**1.945**	**0.137**
	migration~abs(latitude)+logBM+ grow_grass_diet + diet_shift	0.431	6	-102.7	217.9	2.871	0.086
	migration~ (logBM)^2 + grow_grass_diet +temp_seas_mean	0.451	6	-103.5	219.4	4.382	0.041
	migration~ logBM + grow_grass_diet +temp_seas_mean	0.433	5	-105.0	220.2	5.214	0.027
Herbivores < 500 kg (*N* = 192)	***migration~abs(latitude)+logBM+ grow_grass_diet***	**0.449**	**5**	**-88.23**	**186.9**	**0**	**0.299**
	migration~abs(latitude)+logBM+ grow_grass_diet + diet_shift	0.456	6	-87.55	187.6	0.689	0.212
	migration~abs(latitude)+logBM+ grow_grass_diet+mean_temp_sd	0.466	6	-88.47	189.4	2.522	0.085
	migration~logBM+grow_grass_diet +temp_seas_mean	0.459	5	-89.62	189.6	2.693	0.078
	migration~abs(latitude)+logBM+ grow_grass_diet+mean_temp_sd+diet_shift	0.472	7	-87.89	190.4	3.524	0.051
	migration~logBM+grow_grass_diet +temp_seas_mean+diet_shift	0.464	6	-89.14	190.7	3.858	0.043
50 - 500 (*N* = 81)	***migration~abs(latitude)+grow_grass_diet + mean_temp_sd***	**0.482**	**5**	**-39.74**	**90.27**	**0**	**0.302**
	migration~abs(latitude)+ logBM+ grow_grass_diet+mean_temp_sd	0.502	6	-39.24	91.61	1.342	0.154

	migration~abs(latitude) + diet_shift grow_grass_diet + mean_temp_sd	0.483	6	-39.82	92.77	2.501	0.086
	migration~ grow_grass_diet + mean_temp_sd	0.368	4	-42.33	93.19	2.919	0.070
	migration~abs(latitude) + (logBM)^2 grow_grass_diet + mean_temp_sd	0.503	7	-38.83	93.20	2.928	0.070
	migration~abs(latitude) + logBM + diet_shift + grow_grass_diet + mean_temp_sd	0.502	7	-39.39	94.32	4.046	0.040
Ungulates only (*N* =175)	***migration~abs(latitude)+ logBM + grow_grass_diet***	**0.438**	**5**	**-87.99**	**186.3**	**0**	**0.488**
	migration~abs(latitude)+ (logBM)^2 + grow_grass_diet	0.449	6	-87.87	188.2	1.907	0.188
	migration~abs(latitude) + logBM + grow_grass_diet + diet_shift	0.441	6	-87.95	188.4	2.062	0.174
	migration~abs(latitude)+ (logBM)^2 + grow_grass_diet + diet_shift	0.450	7	-88.05	190.8	4.425	0.053
	migration~abs(latitude)+ logBM + grow_grass_diet + mean_temp_sd	0.445	6	-89.96	192.4	6.082	0.023
	migration~abs(latitude)+ (logBM)^2 + grow_grass_diet + mean_temp_sd	0.457	7	-89.79	194.3	7.910	0.009

Table S7. Model selection results for the predictors of dietary shifts using different data subsets. Only the 5-7 highest ranked models are listed. ‘Preferred’ models (all models with $\Delta \mathrm{AIC_c} < 2$) are *italicized*, whereas the ‘best’ model (simplest model with $\Delta \mathrm{AIC_c} < 2$) is **bolded**.

Data set	Model formula	R^2	K	logLik	AICc	ΔAICc	weight
All herbivores with nutrient data (N = 158)	***diet_shift~(grow_grass_diet)^2***	**0.540**	**4**	**178.7**	**-349.1**	**0**	**0.64**
	diet_shift~(grow_grass_diet)^2 + cec_sd	0.576	5	178.8	-347.2	1.879	0.25
	diet_shift~(grow_grass_diet)^2 + nit_mean	0.556	5	177.0	-343.6	5.471	0.042
	diet_shift~(grow_grass_diet)^2 + logBM	0.545	5	175.8	-341.2	7.875	0.012
	diet_shift~(grow_grass_diet)^2 + cec_mean	0.56	5	175.7	-341.0	8.133	0.011
	diet_shift~(grow_grass_diet)^2+ nit_mean + cec_sd	0.588	6	176.7	-340.8	8.350	0.010
	diet_shift~(grow_grass_diet)^2+ migration	0.542	5	175.5	-340.7	8.453	0.009
All herbivores (N = 210)	***diet_shift~(grow_grass_diet)^2***	**0.519**	**4**	**231.8**	-455.4	0	0.949
	diet_shift~(grow_grass_diet)^2 + migration	0.522	5	229.0	-447.4	8.038	0.017
	diet_shift~(grow_grass_diet)^2 + logBM	0.523	5	228.8	-447.4	8.077	0.017
	diet_shift~(grow_grass_diet)^2 + mean_temp_sd	0.526	5	228.4	-446.6	8.878	0.011
	diet_shift~(grow_grass_diet)^2 + (logBM)^2	0.522	5	227.2	-444.0	11.402	0.003
	diet_shift~(grow_grass_diet)^2+abs(latitude)	0.526	5	226.1	-441.9	13.484	0.001
Herbivores < 500 kg (N = 192)	***diet_shift~(grow_grass_diet)^2***	**0.510**	**4**	**210.7**	**-413.2**	**0**	**0.893**
	diet_shift~(grow_grass_diet)^2 + logBM	0.519	5	209.0	-407.7	5.548	0.056
	diet_shift~(grow_grass_diet)^2 + migration	0.516	5	208.3	-406.3	6.876	0.029
	diet_shift~(grow_grass_diet)^2 + (logBM)^2	0.518	5	207.5	-404.6	8.553	0.012
	diet_shift~(grow_grass_diet)^2 + mean_temp_sd	0.514	5	206.7	-403.1	10.072	0.006
	diet_shift~(grow_grass_diet)^2+ abs(latitude)	0.518	5	205.2	-400.1	13.065	0.001
Herbivores 50 - 500 kg (N =81)	***diet_shift~(grow_grass_diet)^2***	**0.549**	**4**	**80.09**	**-151.6**	**0**	**0.948**
	diet_shift~(grow_grass_diet)^2 + logBM	0.549	5	77.68	-144.6	7.082	0.027
	diet_shift~(grow_grass_diet)^2 + migration	0.549	5	77.19	-143.6	8.063	0.017
	diet_shift~(grow_grass_diet)^2 + (logBM)^2	0.549	5	76.22	-141.6	10.01	0.006
	diet_shift~(grow_grass_diet)^2 + mean_temp_sd	0.550	5	75.90	-141.0	10.653	0.005
	diet_shift~(grow_grass_diet)^2+abs(latitude)	0.557	5	74.25	-137.7	13.934	0.001
	diet_shift~(grow_grass_diet)^2+ rainfall_seas_mean	0.563	5	74.20	-137.6	14.038	0.001
Ungulates only (N =175)	***diet_shift~(grow_grass_diet)^2***	**0.524**	**4**	**189.3**	**-370.3**	**0**	**0.946**
	diet_shift~(grow_grass_diet)^2 + mean_temp_sd	0.536	5	186.8	-363.2	7.173	0.026
	diet_shift~(grow_grass_diet)^2 + migration	0.524	5	186.0	-361.6	8.742	0.012
	diet_shift~(grow_grass_diet)^2 + logBM	0.524	5	185.8	-361.2	9.176	0.010
	diet_shift~(grow_grass_diet)^2 + (logBM)^2	0.524	5	184.4	-358.4	11.935	0.002

Table S8. Sensitivity analysis. The results of statistical tests for differences between tropical and extratropical herbivores if 35° N/S is used as the boundary and if 23.5° N/S is used as the boundary. Qualitatively, results are largely the same regardless of the boundary used to distinguish taxa. 'phylANOVA' refers to phylogenetic analysis of variance, which tests for differences between group means; and 'KS test' to a Kolmogorov–Smirnov test, which tests for differences between group distributions. Significantly different results ($P < 0.05$) are **bolded**.

Dependent variable	Dataset (N)	**35° N/S**				**23.5° N/S**			
		phylANOVA		KS test		phylANOVA		KS test	
		F	P	D	P	F	P	D	P
Body size	Nutrient (158)	0.1127	0.793	0.2564	**0.0142**	2.8237	0.631	0.2003	0.1029
	Full (210)	0.8235	0.591	0.2625	**0.0105**	2.1898	0.611	0.1594	0.1447
	< 500 kg (192)	3.6031	0.180	0.2936	**0.0064**	0.2891	0.893	0.1337	0.3631
	50 - 500 kg (81)	1.4227	0.401	0.2983	0.0991	0.3775	0.647	0.2090	0.3548
	Ungulates (175)	0.7582	0.541	0.2627	**0.0263**	0.0669	0.901	0.1896	0.0990
Grass dependence	Nutrient (158)	1.0793	0.410	0.2313	0.1823	0.7591	0.821	0.2212	0.0537
	Full (210)	0.4439	0.712	0.1840	0.1756	1.6935	0.697	0.2618	**0.0016**
	< 500 kg (192)	0.3987	0.737	0.2023	0.1303	2.0363	0.686	0.2870	**7.88×10^{-4}**
	50 - 500 kg (81)	3.3761	0.178	0.3487	**0.0329**	0.7053	0.549	0.2522	0.1625
	Ungulates (175)	0.0219	0.920	0.2044	0.1451	0.2118	0.814	0.2847	**0.0023**
Migration	Nutrient (158)	17.433	**0.003**	0.4060	**0.0012**	2.1975	0.702	0.1175	0.6877
	Full (210)	33.537	**0.001**	0.4438	**1.43×10^{-6}**	8.0139	0.259	0.1912	**0.0456**
	< 500 kg (192)	36.796	**0.001**	0.4690	**8.42×10^{-7}**	11.146	0.165	0.2296	**0.0133**
	50 - 500 kg (81)	11.609	**0.007**	0.3728	**0.0183**	15.759	**0.005**	0.3930	**0.0045**
	Ungulates (175)	37.108	**0.001**	0.4955	**4.05×10^{-7}**	21.760	**0.009**	0.3415	**1.17×10^{-4}**
Dietary shifts	Nutrient (158)	7.1917	**0.030**	0.3789	**0.0032**	12.513	0.147	0.3717	**7.33×10^{-5}**
	Full (210)	10.115	**0.013**	0.3634	**0.0001**	23.735	**0.009**	0.3893	**3.14×10^{-7}**
	< 500 kg (192)	13.346	**0.006**	0.4117	**2.44×10^{-5}**	27.828	**0.005**	0.4099	**2.29×10^{-7}**
	50 - 500 kg (81)	14.229	**0.002**	0.5351	**0.0001**	11.411	**0.014**	0.4456	**7.93×10^{-4}**
	Ungulates (175)	12.601	**0.011**	0.4183	**3.39×10^{-5}**	36.144	**0.001**	0.4662	**2.57×10^{-8}**

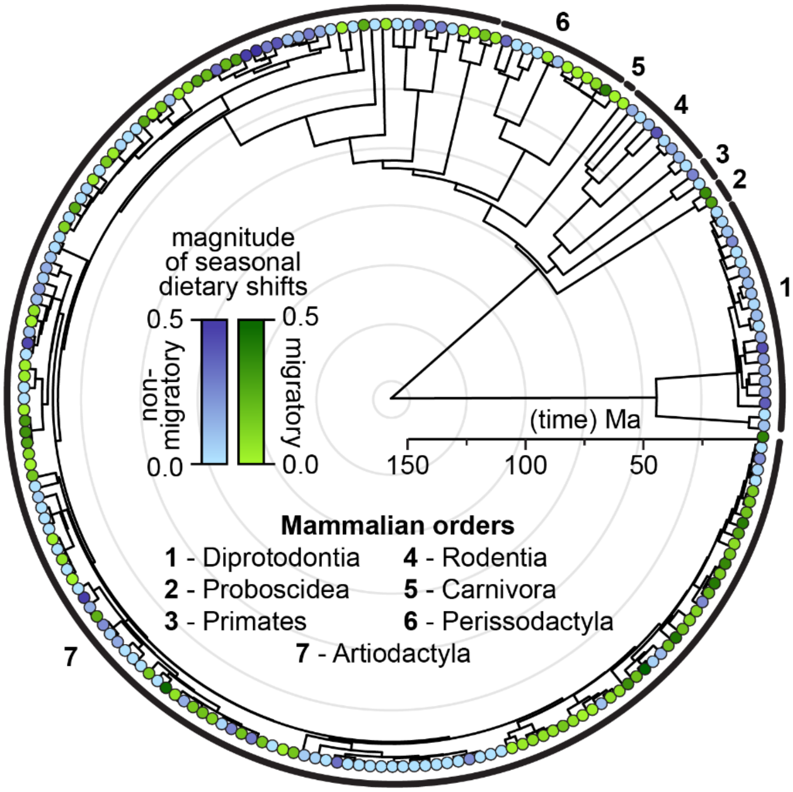

Figure S1. Phylogenetic distribution of seasonal strategies. Point colors at the tips of the phylogeny correspond to herbivore seasonal strategies, where *blue* points correspond to non-migratory herbivores, *green* points correspond to migratory herbivores, and *darker* points reflect species that exhibit larger seasonal diet shifts. *Light grey* circles correspond to 25 Ma intervals. Numbers around the margins of the phylogeny correspond to herbivore orders.

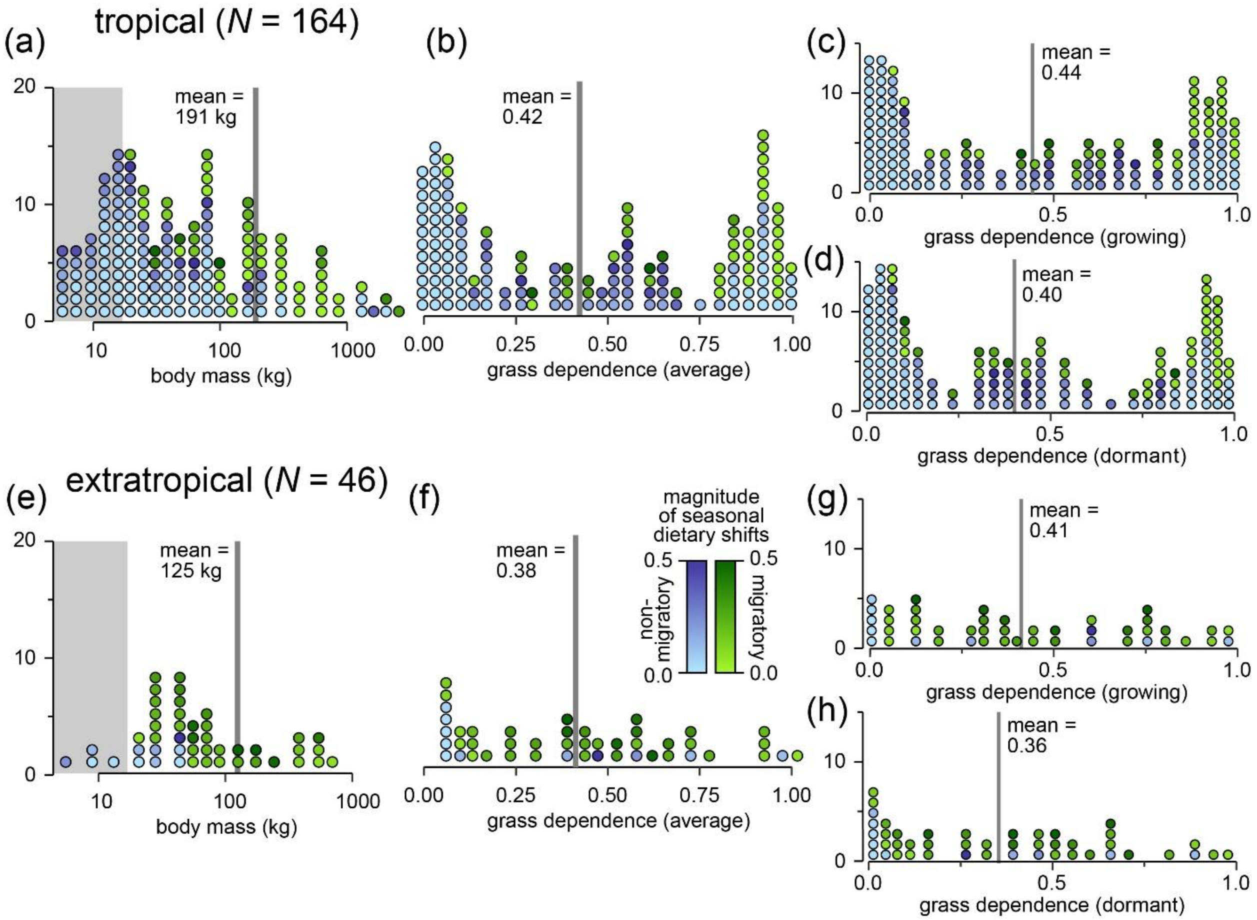

Figure S2. Trait distributions for tropical (*a-d*) and extratropical herbivores (*e-g*). For both, body mass distributions are roughly unimodal (*a,e*), with means between 100-200 kg, though the body mass distribution is significantly narrower for temperate herbivores. In contrast, dietary distributions are roughly trimodal for both extratropical and tropical herbivores (*b,f*), with a mean dietary grass fraction of *ca.* 0.40. This is particularly evident in the dormant season (*d,h*) as compared to the growth season (*c,g*), when diet distributions become flatter (possibly suggesting that herbivore niche breadths increase in the dormant season when resources are scarce). Note that extratropical herbivores seasonally shift their diets significantly more than do tropical herbivores. *Dark grey* lines correspond to means (none of which differ significantly between temperate and tropical herbivores). Point colors correspond to herbivore seasonal strategies, where *blue* points correspond to non-migratory herbivores, *green* points correspond to migratory herbivores, and *darker* points reflect species that exhibit larger seasonal diet shifts. *Light grey* boxes in (*a,e*) correspond to regions of trait space where no herbivores exhibit migratory behavior, possibly suggesting some morphological and/or energetic constraint on migration.