LETTER

ECOLOGY LETTERS | cnrs WILEY

Body size and digestive system shape resource selection by ungulates: A cross-taxa test of the forage maturation hypothesis

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BODY SIZE AND DIGESTIVE SYSTEM SHAPE RESOURCE SELECTION BY UNGULATES: A
CROSS-TAXA TEST OF THE FORAGE MATURATION HYPOTHESIS

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Editor: Jean-Michel Gaillard

Abstract

The forage maturation hypothesis (FMH) states that energy intake for ungulates is maximised when forage biomass is at intermediate levels. Nevertheless, metabolic allometry and different digestive systems suggest that resource selection should vary across ungulate species. By combining GPS relocations with remotely sensed data on forage characteristics and surface water, we quantified the effect of body size and digestive system in determining movements of 30 populations of hindgut fermenters (equids) and ruminants across biomes. Selection for intermediate forage biomass was negatively related to body size, regardless of digestive system. Selection for proximity to surface water was stronger for equids relative to ruminants, regardless of body size. To be more generalisable, we suggest that the FMH explicitly incorporate contingencies in body size and digestive system, with small-bodied ruminants selecting more strongly for potential energy intake, and hindgut fermenters selecting more strongly for surface water.

KEYWORDS
Equidae, forage biomass, hindgut fermentation, macroecology, ruminant, step-selection function, water requirements

INTRODUCTION

Animal movements should be influenced by the need to maintain a positive balance between energetic gains and losses (Middleton et al., 2013; Nathan et al., 2008; Owen-Smith et al., 2010; Senft et al., 1987). Foraging behaviours employed by ungulates vary according to body size and digestive system (ruminant vs. hindgut fermenters; Bell, 1971; Demment & Van Soest, 1985; Hopcraft et al., 2012; Olff et al., 2002). Smaller-bodied ungulates (i.e. ruminants, primarily) should forage in patches with highly digestible forage (high energy and nutrient concentrations) because they possess high mass-specific metabolic rates. In contrast, larger-bodied ungulates (i.e. both larger-bodied ruminants and hindgut fermenters)

should forage in high biomass patches because of higher absolute energy demands (Barboza & Bowyer, 2000; Illius & Gordon, 1992; Jarman, 1974; McNab, 1974). Consequently, body size creates trade-offs in how ungulates should prioritise forage biomass and forage digestibility (Bailey et al., 1996; Olff et al., 2002; Wilmshurst et al., 2000).

For nearly 30 years, the forage maturation hypothesis (hereafter, 'FMH'; Fryxell, 1991) has provided a lens for understanding resource selection and movements of free-ranging ungulates (Fryxell, 1991; Hebblewhite et al., 2008; Merkle et al., 2016). Digestibility of forage is highest at the beginning of the growing season because plants lack structural fibre needed to support high biomass (Van Soest, 1996). At this earliest phenological stage, however,

plants are small and biomass is limiting, so energy intake of ungulates may be limited by bite size (Hebblewhite et al., 2008; Spalinger & Hobbs, 1992; Wilmshurst et al., 2000). Digestibility then declines as plants mature, gain biomass and become more fibrous (Van Soest, 1996). Because of this phenological trade-off between biomass and digestibility of plants, and according to the FMH, energy intake is maximised for ungulates at intermediate phenological stages (i.e. when rates of both forage intake and digestibility are at intermediate levels; Figure 1a). Although the FMH was originally developed to explain resource selection in tropical, bulk-grazing ruminants, its predictions are relevant for temperate ruminants that display a diversity of feeding strategies (e.g. unselective grazing, selective browsing and mixed feeding; Albon & Langvatn, 1992; Hofmann, 1989; Middleton

et al., 2018; Mueller et al., 2008). As a result, the FMH frequently forms the basis for conceptualising resource selection and movements of ungulates – including large- and small-bodied species, and hindgut and ruminant fermenters – across the globe (e.g. Drescher et al., 2006; Edouard et al., 2010; Fleurance et al., 2010; St-Louis & Cote 2014).

The central prediction of the FMH – that ungulates should select forage of intermediate biomass and intermediate digestibility to maximise energy intake – should hinge largely on body size. In 1971, Bell first articulated how metabolic rate should interact with resource selection by free-ranging ungulates, stating that relative requirements (i.e. energy and protein per unit weight and per unit time) are higher for smaller ungulates, while absolute requirements (i.e. energy and protein per
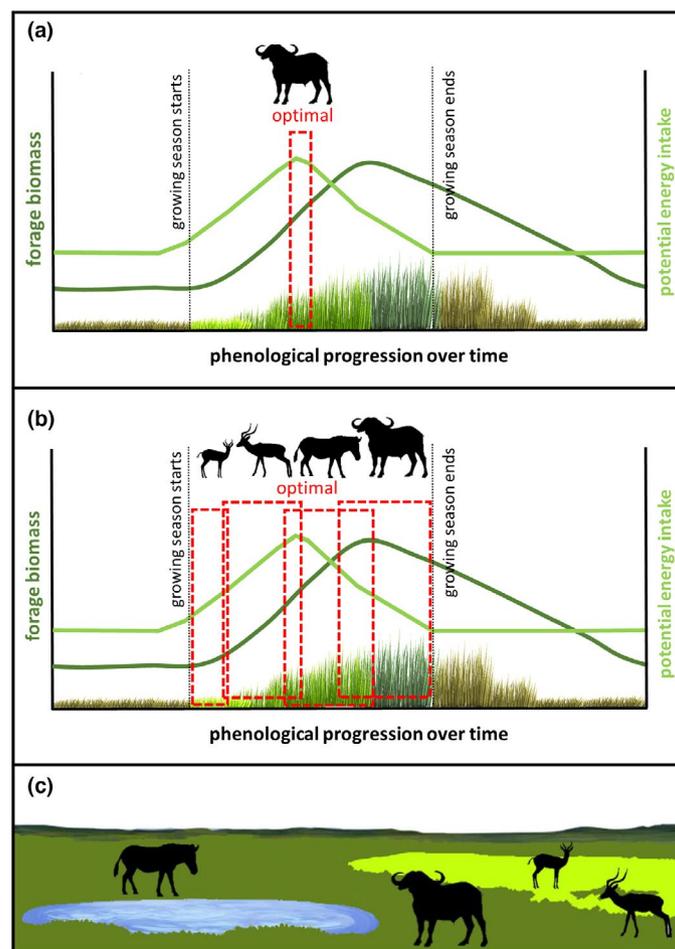
FIGURE 1 Illustrated predictions for resource selection by equids and different sizes of ruminants during a hypothetical growing season and in a hypothetical landscape. Forage biomass (dark green line) and potential energy intake (light green line; measured by rate of change in forage biomass) increase at beginning of the growing season. The potential for maximum energy intake occurs at the middle of the growing season, when forage biomass is at intermediate levels. Different sizes and shades of grass represent phenological stages of forage biomass and digestibility. At early phenological stages (i.e. the lightest shade of green grass), potential energy intake is low because forage biomass is low. At late phenological and senescent stages (i.e. the darkest shade of green grass and brown grass, respectively), potential energy intake is low because forage digestibility is low. (a) The forage maturation hypothesis predicts that ungulates maximise their energy intake by selecting forage of intermediate biomass at intermediate phenological stages. (b) However, selection for forge characteristics should also depend on body size. (c) Smaller-bodied ungulates (which exhibit ruminant digestion) should select most strongly for maximal energy intake (light green), larger-bodied ruminants should select for forage biomass (dark green) and equids should select for surface water (blue) to meet their physiological needs

individual and per unit time) are higher for larger ungulates (Bell, 1971). Over two decades ago, Wilmshurst et al., (2000) extended the work of Bell (1971) and Fryxell (1991) by testing quantitative predictions for selection of optimal biomass by five co-occurring ruminants in Serengeti National Park. Wilmshurst et al., (2000) predicted that optimal biomass of plants selected by large herbivores would vary as a function of body size, at least among ruminants. Specifically, resource selection should occur along a gradient from high digestibility/low biomass to low digestibility/high biomass, dependent on body size. Explicitly considering and testing for this contingency among a diversity of ungulates would refine the predictive capacity of the FMH, thereby advancing its application to ungulates more generally (Figure 1a, b).

In addition to forage biomass and energy content, reliance on surface water restricts the movement and distribution of ungulates across some landscapes (Rozen-Rechels et al., 2019; Veldhuis et al., 2019). Ruminants efficiently extract protein from fresh plant tissue because the fermentation site (rumen) occurs anterior to the absorption site (small intestine) for proteins. Ruminants, therefore, employ an 'efficient' urea cycle in which available nitrogen is recycled throughout the digestive tract, thereby conserving water (Janis, 1976; Owens & Basalan, 2016; Santos et al., 2011). In contrast, hindgut fermenters have reduced retention time, but lower rates of protein extraction (Duncan et al., 1990; Janis, 1976; Van Soest, 1996). Consequently, hindgut fermenters excrete more urea, which must be accompanied by water. Larger-bodied ungulates – and larger-bodied hindgut fermenters in particular – consume large amounts of biomass and should, therefore, be further tied to surface water (i.e. water available for drinking, as opposed to contained within plants) because high biomass forage tends to be drier (Bell, 1971; Redfern et al., 2003; Schoenecker et al., 2016). Therefore, constraints associated with conserving water in the body should tie hindgut fermenters to water, and potentially result in deviations from the central prediction of the FMH (which is based purely on biomass and digestibility of forage). In sum, natural selection should favour ungulate movements that optimise net energy gain despite constraints imposed by forage biomass, the energy contained within forage and surface water, with the relative importance of each arising as a function of body size and digestive system (Redfern et al., 2003; Figure 1b, c).

We tested the central prediction of the FMH by linking high-resolution movement trajectories (unavailable when the FMH was conceptualised) with selection of forage biomass, potential energy intake and surface water by free-ranging ungulates. We evaluated the relative influence of body size and digestive system on selection for these resources by ruminants (foregut fermenters) and equids (family Equidae, representing hindgut fermenters) using GPS telemetry data from 30 populations of 19 species distributed across the biomes. We predicted

that (1) smaller-bodied ungulates (all of which exhibit ruminant fermentation) would select for resource patches that maximise energy intake, thereby conforming to the central prediction of the FMH (Figure 1a); whereas, (2) by virtue of their larger body size, resource selection patterns of both larger-bodied ruminants and equids would deviate from this prediction (Figure 1b). Specifically, we expected that larger-bodied ruminants would select most strongly for patches of high forage biomass, whereas equids (because of their hindgut fermentation) would select most strongly for patches close to water.

METHODS

Data collection

We compiled a global dataset of GPS locations for 11 populations of equids and 19 populations of ruminants totalling 580 individuals; data for all study populations were collected between 2005 and 2019 (Figure 2a; Table S1). The equid dataset comprised GPS relocations for seven (of nine) extant species of wild and feral equids: Asiatic wild ass (khulan, *Equus hemionus hemionus* and onager, *E. h. onager*), feral burro (*E. asinus*), feral horse (*E. caballus*), Grevy's zebra (*E. grevyi*), mountain zebra (*E. zebra*), plains zebra (*E. quagga*) and Przewalski's horse (*E. ferus*). The ruminant dataset included GPS relocations for 12 species: African buffalo (*Syncerus caffer*), elk (*Cervus canadensis*), goitered gazelle (*Gazella subgutturosa*), impala (*Aepyceros melampus*), Mongolian gazelle (*Procapra gutturosa*), mule deer (*Odocoileus hemionus*), red deer (*Cervus elaphus*), reindeer (*Rangifer tarandus tarandus*), roe deer (*Capreolus capreolus*), saiga antelope (*Saiga tatarica*), springbok (*Antidorcas marsupialis*) and white-bearded wildebeest (*Connochaetes taurinus*). Equid species ranged in body size from 180 kg (feral burro) to 430 kg (feral horse; Wilson & Mittermeier, 2011); ruminant species ranged in body size from 24 kg (roe deer) to 592 kg (African buffalo; Wilson & Mittermeier, 2011). Hereafter, we distinguish between 'study areas' (the geographic locales in which resource selection were quantified) and 'study populations' (individuals fitted with GPS collars within a study area; Table S1). Five of our study areas contained multiple study populations, and eight species were represented by two or more study populations spread across different study areas (Table S1). Inaccurate GPS locations were removed either by co-authors or by excluding locations with dilution of precision >10.

We restricted our analyses to habitats with minimal canopy cover, including rangelands, savannahs, open forest, and tundra. We intended to include sufficiently open canopies for remotely sensed vegetation indices to work properly. Therefore, we applied two criteria in selecting study populations. The first criterion required that a study area be comprised of <20%
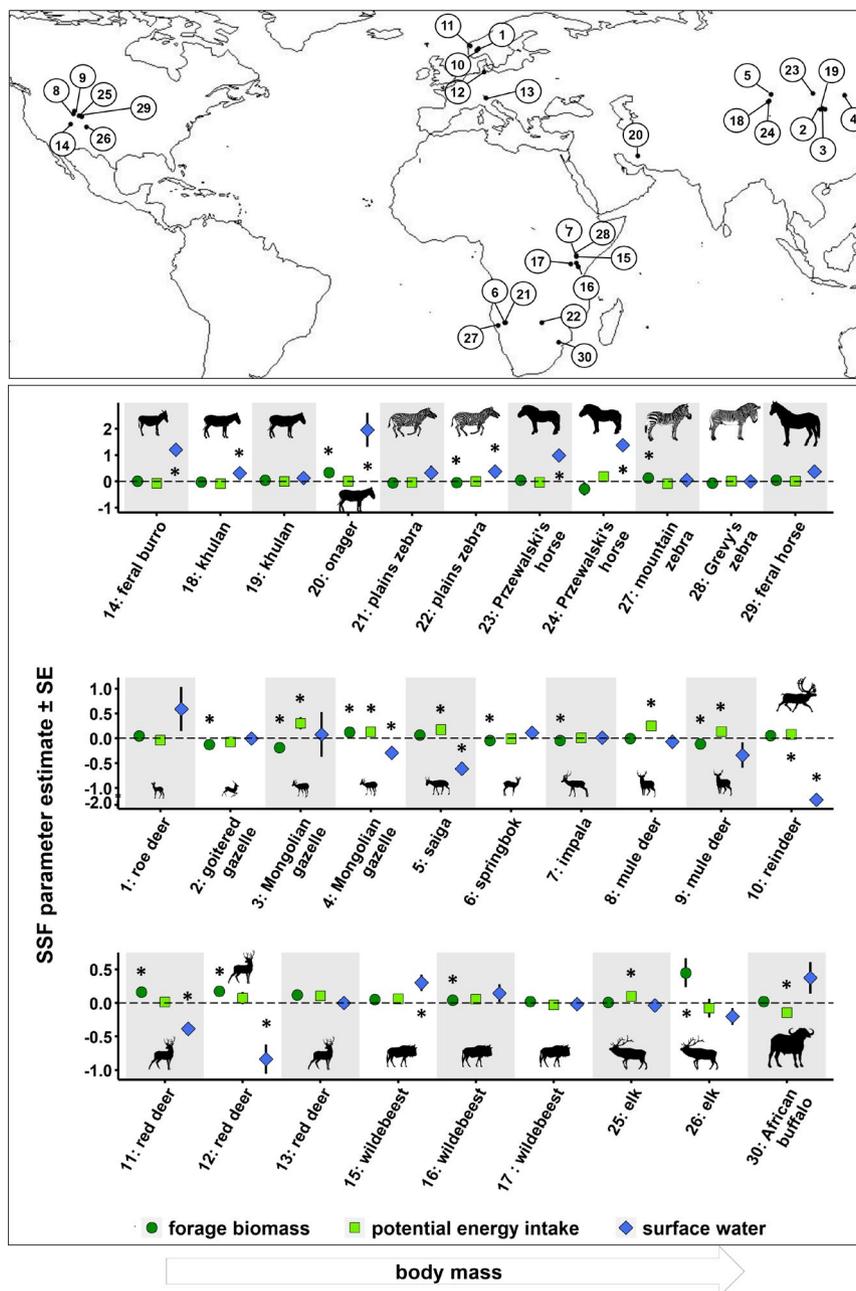
FIGURE 2 Locations of the study populations (top panel) and mean ± SE parameter estimates of step-selection functions (SSF) for 11 populations of equids (second panel) and 19 populations of ruminants (third and fourth panels) during growing seasons. Significant variables with 95% confidence intervals excluding zero are marked by asterisks. Populations are numbered in increasing order of a focal species' body size: 1 – roe deer (*n* = 23); 2 – goitered gazelle (*n* = 6); 3 –Mongolian gazelle (*n* = 7); 4 – Mongolian gazelle (*n* = 5); 5 – saiga (*n* = 26); 6 – springbok (*n* = 10); 7 – impala (*n* = 21); 8 – mule deer (*n* = 100); 9 – mule deer (*n* = 78); 10 – reindeer (*n* = 25); 11 – red deer (*n* = 51); 12 – red deer (*n* = 22); 13 – red deer (*n* = 13); 14 – feral burro (*n* = 10); 15 – wildebeest (*n* = 9); 16 – wildebeest (*n* = 12); 17 – wildebeest (*n* = 13); 18 – khulan (*n* = 7); 19 – khulan (*n* = 9); 20 – onager (*n* = 9); 21 – plains zebra (*n* = 9); 22 – plains zebra (*n* = 31); 23 –Przewalski's horse (*n* = 14); 24 – Przewalski's horse (*n* = 5); 25 – elk (*n* = 20); 26 – elk (*n* = 7); 27 – mountain zebra (*n* = 5); 28 – Grevy's zebra (*n* = 7); 29 – feral horse (*n* = 22) and 30 – African buffalo (*n* = 4)

'dense forest', as classified by the Food and Agriculture Organization (FAO; Friedl & Sulla-Menashe, 2015). The second criterion required that per cent (%) tree cover across the entire study area was <40% (Hansen et al., 2013; Table S1). We calculated per cent of the study area covered with dense forest and mean % tree cover within minimum convex polygons (MCP) constructed for

each study population using the Terra and Aqua combined Moderate Resolution Imaging Spectroradiometer (MODIS), Land Cover Type, MCD12Q1, Version 6, layer 7, spatial resolution of 500 metres and temporal resolution of a year (Friedl & Sulla-Menashe, 2015) and Global 2010 Tree Cover (spatial resolution 30 m, Hansen et al., 2013) respectively.

Forage biomass and potential energy intake

To delineate study areas, we computed the MCP around each population's GPS locations and buffered the MCP's bounding box by 5 km to ensure that we captured adjacent habitats that were available to telemetered individuals. Within each study area, we extracted modified soil-adjusted vegetation index (MSAVI; MODIS terra satellite imagery, version 6.0 MOD09Q1; spatial resolution 250 × 250 m and temporal resolution 8 days) using the MSAVI2 method and equations described in Qi et al., (1994) as a proxy of forage biomass (Borowik et al., 2013; Pettorelli et al., 2005). In arid environments, MSAVI and other soil-adjusted indices of vegetation are more appropriate than the more commonly used normalised difference vegetation index (NDVI) because they minimise the influence of bare ground on estimates of vegetation (Qi et al., 1994). Additionally, NDVI and MSAVI are extracted from similar spectral bands, and usually are strongly correlated in temperate conditions (Jin et al., 2014; Liang et al., 2016). We removed pixels categorised as snow, cloud or shadow using quality assessment bands, then smoothed each time series of MSAVI using a moving three-scene median filter and applied a linear interpolation (Branco et al., 2019).

To estimate the instantaneous rate of green-up (IRG), we calculated the rate of change in MSAVI for every three consecutive dates by using a three-scene moving window (Avgar et al., 2013; Branco et al., 2019). The IRG is a metric that combines both forage biomass and forage digestibility, which collectively equate to potential energy intake (i.e. a proxy of energy that could be effectively available to the feeder, Avgar et al., 2013; Bischof et al., 2012; Geremia et al., 2019). The IRG is positively correlated with the peak in faecal crude protein in ungulates (Hamel et al., 2009) and has been used widely as an index of the energy contained in forage across space and time (Branco et al., 2019; Merkle et al., 2016; Rivrud et al., 2016); days from peak IRG is strongly correlated with N:C ratios in grasses (Geremia et al., 2019). Hereafter, we refer to selection for IRG as selection for 'potential energy intake'. Similarly, and hereafter, we refer to selection for peak biomass of forage as simply selection for 'forage biomass'. Although IRG combines both forage biomass and forage digestibility, it is not redundant with metrics that solely represent forage biomass: while high IRG values represent intermediate plant biomass, low values of IRG may represent either low or high biomass (see Figure 1a). We, therefore, used both IRG and MSAVI to disentangle selection for potential energy intake and forage biomass. We normalised both MSAVI and IRG values between 0 and 1 based on the lowest and highest value of each pixel in a year, respectively. Thus, for each pixel, an MSAVI value of 1 represented the highest biomass and a value of 0 represented the lowest biomass in a given year, for a given study population. Similarly, an IRG value of 1 represents forage at a state of intermediate biomass (and the peak rate of green-up), whereas an IRG value of 0 represents forage at a low rate of change. Collectively, these two layers, therefore, represent metrics of plant phenology across space and time (see also Bischof et al., 2012; Branco et al., 2019; Merkle et al., 2016).

To evaluate how body size and digestive system influenced resource selection, we temporally constrained our analysis times when plants were actively growing (to ensure positive IRG was available to the animals). We determined the duration of growing seasons in each study population by randomly generating 10,000 points within each study area, extracting absolute (non-normalised) MSAVI and IRG values associated with each of the random points and plotting annual MSAVI and IRG profiles (Figure S1). For study areas with a single 'growing season' per year (25 of 30 study populations), we defined the beginning of the 'growing season' as the Julian day when IRG became positive for three consecutive scenes, and the end of the 'growing season' as the Julian day when IRG reached the minimum negative point, followed by IRG values less than or equal to zero (Figure S1a; *sensu* Jesmer et al., 2018). For study areas with multiple growing seasons per year, we attempted to define each 'growing season' consistent with the method described above (Figure S1b). We then filtered our dataset to only those relocations that occurred during growing seasons (Table S1).

Distance to surface water

Fine-scale data on surface water is challenging to acquire via remote sensing because of computational restrictions (Huang et al., 2018; Pekel et al., 2016; Redfern et al., 2003). Furthermore, globally collected precipitation data may underestimate water available to wildlife, given artificial water sources (Ogutu et al., 2010). We treated the distribution of surface water as fixed throughout each growing season. We used the following data to identify the occurrence of surface water:

1-Remotely sensed data on surface water

We used monthly data from the Global Surface Water Explorer (Pekel et al., 2016) to estimate occurrence of surface water during the growing season for each study area. With a spatial resolution of 30 x 30 m and temporal resolution of 1 month, the Global Surface Water Explorer constitutes the most precise data on the distribution of surface water (Pekel et al., 2016). For each study area and growing season, we extracted monthly time series of pixels, where each pixel was assigned a 1 or 0, indicating presence versus absence of surface water. We then merged monthly layers into a single layer of surface water.

2-Locally collected data on surface water

To increase accuracy of our estimates of surface water for each study population, we compiled data on springs, streams, small ponds and man-made water sources (i.e. surface water sources <30 × 30 m that were undetectable using the Global Water Surface Explorer; Text S1 and Table S2). We merged the locations of locally collected surface water with the layer on remotely sensed data on surface water. We then generated a distance to surface water layer by calculating linear distances between centroids of pixels classified as 'surface water' and centroids of non-surface water pixels. To ensure that our distance to surface water layer occurred at a comparable scale with MSAVI and IRG, we normalised values for distance to surface water between 0 and 1 for each study area based on the lowest and highest value of pixels in each growing season respectively.

Statistical analyses

We built step-selection functions (Avgar et al., 2016; Thurfjell et al., 2014) to quantify how spatiotemporal patterns of forage biomass, potential energy intake and surface water influenced movements by ungulates in each study population during growing seasons. To meet the assumption that the speed of successive steps was uncorrelated (since the step-selection method assumes Brownian motion), we used the R package CTMM (Calabrese et al., 2016) to estimate the average time at which 99% of the correlation in speed between successive steps had decayed (i.e. about 3 times of tauV; Fleming et al., 2014) in each population. We then rarified (i.e. temporally subsampled) the GPS locations of each population, which resulted in uncorrelated, successive steps (Table S1; Dupke et al., 2017; Fleming et al., 2014). For each observed (used) step, we generated 100 potential (unused) steps by fitting a gamma and von Mises distribution to the step lengths and turning angles, respectively (Signer et al., 2019), and then compared observed and potential steps using conditional logistic regression (Fortin et al., 2005). In addition to step length (standardised to a mean of 0.0 and standard deviation of 1.0), we extracted values of forage biomass, potential energy intake and distance to surface water at the end points of each observed and potential step. We used conditional logistic regression to estimate selection coefficients, with each stratum consisting of an observed step and its associated 100 potential steps, and each individual as an independent cluster in fitting a separate model for each study population (Merkle et al., 2016; Prima et al., 2017; Roever et al., 2010). Correlation among the independent variables was minimal (mean r between MSAVI and IRG = −0.09, range = −0.34 to 0.20; mean r between MSAVI and distance to surface water = 0.02, range = −0.17 to 0.55; mean r between IRG and distance

to water = 0.008, range = −0.28 to 0.22; Table S3). Since layers for forage biomass and potential energy intake encompassed both spatial and temporal variation across landscapes, but surface water layers encompassed only spatial variation across landscapes, we did not include interactions between forage biomass and water, or between potential energy intake and water in our analyses. Furthermore, we did not find a significant correlation between selection for forage biomass and availability of surface water (i.e. mean distance to surface water; left panel of Figure S3), or did we find a significant correlation between selection for potential energy intake and mean distance to surface water (right panel of Figure S3). Sample sizes (numbers of individuals telemetered and the range in numbers of individuals telemetered for a given year) are presented for each study population in Table S1. We interpreted that significant, positive selection for IRG was indicative of movements consistent with the FMH (Aikens et al., 2017; Merkle et al., 2016). We considered variables significant in the models when 95% confidence intervals around parameter estimates did not encompass zero. We performed these analyses using packages 'amt' and 'survival' in Program R (R Core Team, 2019; Signer et al., 2019; Therneau & Lumley, 2015).

We next tested the effect of body size and digestive system (i.e. equids or hindgut fermenters vs. ruminants or foregut fermenters) on resource selection across populations using weighted least-square regressions and analysis of covariance (ANCOVA). Because resource selection may intensify when a particular resource is scarce, variable or both (i.e. functional responses in habitat selection [Holbrook et al., 2019; Mysterud & Ims, 1998]), we performed pairwise correlations between population-level selection coefficients for each resource and the (1) mean value of MSAVI, IRG and distance to surface water; and (2) the coefficient of variation (CV) of MSAVI, IRG and distance to surface water. We did not find strong support for functional responses in resource selection (i.e. the effect of resource availability and variability on resource selection; Figure S2), so we attributed variation in selection coefficients to some combination of body size and digestive system. For each of the above tests, we used the parameter estimates derived from the step-selection functions as response variables, and the number of telemetered individuals in each population as a weighting factor. Second, we used weighted ANCOVA to control for the effect of body size (i.e. mean species-specific, sex-unspecific body weight of an adult; Wilson & Mittermeier, 2011) in resource selection. When we did not find a statistically significant effect of digestive system on resource selection after controlling for body size, we pooled equids and ruminants into weighted regression models to test how resource selection was influenced by body size. When the effect of digestive system on resource selection was statistically significant after controlling for body size, we used weighted regression models with body size as a predictor for equids and

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ruminants separately. We switched the direction of parameter estimates for distance to surface water in all analyses and graphs. Therefore, positive and negative values show selection and avoidance for forage biomass, potential energy intake and surface water respectively.

RESULTS

Forage biomass, potential energy intake, distance to surface water or some combination thereof significantly influenced resource selection in 23 of 30 equid and ruminant populations (Figure 2; Table S4). Selection for forage biomass was exhibited by two equids (18%) and five ruminants (26%); avoidance of forage biomass was exhibited by one equid (1%) and five ruminants (26%). Seven ruminants (37%) and no equids selected for potential energy intake (i.e. had movement consistent with the FMH), and one ruminant (0.5%) avoided potential energy intake. Six of eleven equids populations (55%) selected for surface water, with ten of eleven equid populations (91%) having a positive parameter estimates for surface water (Figure 2). Ruminant populations displayed a diversity of selection behaviours towards surface water. Overall, equids consistently selected for surface water, while resource selection of ruminants was variable (Figure 2).

After controlling for the effect of body size, we did not detect any difference in selection for forage biomass ($p = 0.18$; Figure 3a) or potential energy intake ($p = 0.37$; Figure 3c) between equids and ruminants. Body size did not explain variation in selection for forage biomass (Figure 3b) but did explain 25% of the variation in selection for potential energy intake (Figure 3d). Equids selected for surface water more strongly than ruminants after controlling for the effect of body size ($F_{(1,27)} = 7.09$, $p = 0.013$; Figure 3e). Body size did not explain selection for surface water in equids and ruminants ($p \geq 0.23$; Figure 3f and g).

DISCUSSION

We quantified how selection for forage biomass, potential energy intake and surface water shaped the movements of free-ranging ungulates across the globe. In support of the FMH, selection for potential energy intake (i.e. intermediate forage biomass and intermediate forage digestibility) was most frequent among smaller-bodied ungulates. Selecting forage at early to intermediate states of phenology reflects the higher mass-specific energetic requirements of smaller-bodied ungulates (Hopcraft et al., 2012; Illius & Gordon, 1987). In contrast, larger-bodied ungulates (comprising both equids and larger-bodied ruminants) foraged in a manner distinct from the central prediction of the FMH. In accordance with our expectations based on hindgut

fermentation, equids selected consistently for proximity to surface water. In contrast to our expectations based on ruminant digestion coupled with higher absolute energetic requirements, larger-bodied ruminants did not consistently select for forage biomass. We offer two explanations for equivocal support of the hypothesis that larger-bodied ruminants should prioritise high forage biomass: (1) methodological limitations and (2) taxonomic and functional diversity.

Combined with high-resolution data from GPS-telemetered individuals, remotely sensed vegetation indices allow for testing of the FMH across study populations (Wilmers et al., 2013). However, methodological limitations are inherent to such indices, and synthetic studies like ours should be viewed as complementary to (rather than as a substitute for) intensive, field-based investigations, in which forage biomass and quality are quantified directly (e.g. Geremia et al., 2019; Hebblewhite et al., 2008; Wilmshurst et al., 2000). This is particularly the case when remotely sensed vegetation indices – MSAVI and its derivative, IRG – are assumed to be correlated with forage biomass and potential energy intake. Although we did not validate these metrics against field-collected data on forage biomass and potential energy intake (i.e. forage quality), several studies have quantified relationships among forage biomass, forage quality and remotely sensed metrics directly (e.g. Geremia et al., 2019; Hebblewhite et al., 2008; Wilmers et al., 2013), and found that such metrics are suitable representations of forage biomass and quality. Therefore, we believe that MSAVI and IRG (i.e. remotely sensed metrics) are reasonable proxies for forage biomass and potential energy intake, and they are the only way (with which we are familiar) to conduct standardised tests of the FMH across many study populations that range across entire landscapes. A major challenge for future research is to couple field validations of remotely sensed vegetation indices with the high-resolution movement trajectories afforded by GPS telemetry.

Additionally, and at the spatial scale of MODIS, such indices cannot distinguish between sources of 'greenness' resulting from different vegetation types, such as woody plants and grasses (Archibald & Scholes, 2007; Gaughan et al., 2013). So, pixel values could be associated with vegetation that did not necessarily represent forage from an ungulate's perspective. We attempted to minimise the effect of this potential limitation by restricting our analysis to defined growing seasons, and by restricting our analysis to study areas in which dense forest (per Friedl & Sulla-Menashe, 2015) and % tree cover (per Hansen et al., 2013) were minimal. Because the green-up profile in leaves of woody plants is usually constant, the dramatic change in MSAVI (which we used to define the growing seasons) is mostly associated with the green-up of grasses rather than green-up of woody plants (Archibald & Scholes, 2007; Higgins et al., 2011). Therefore, the potential for such
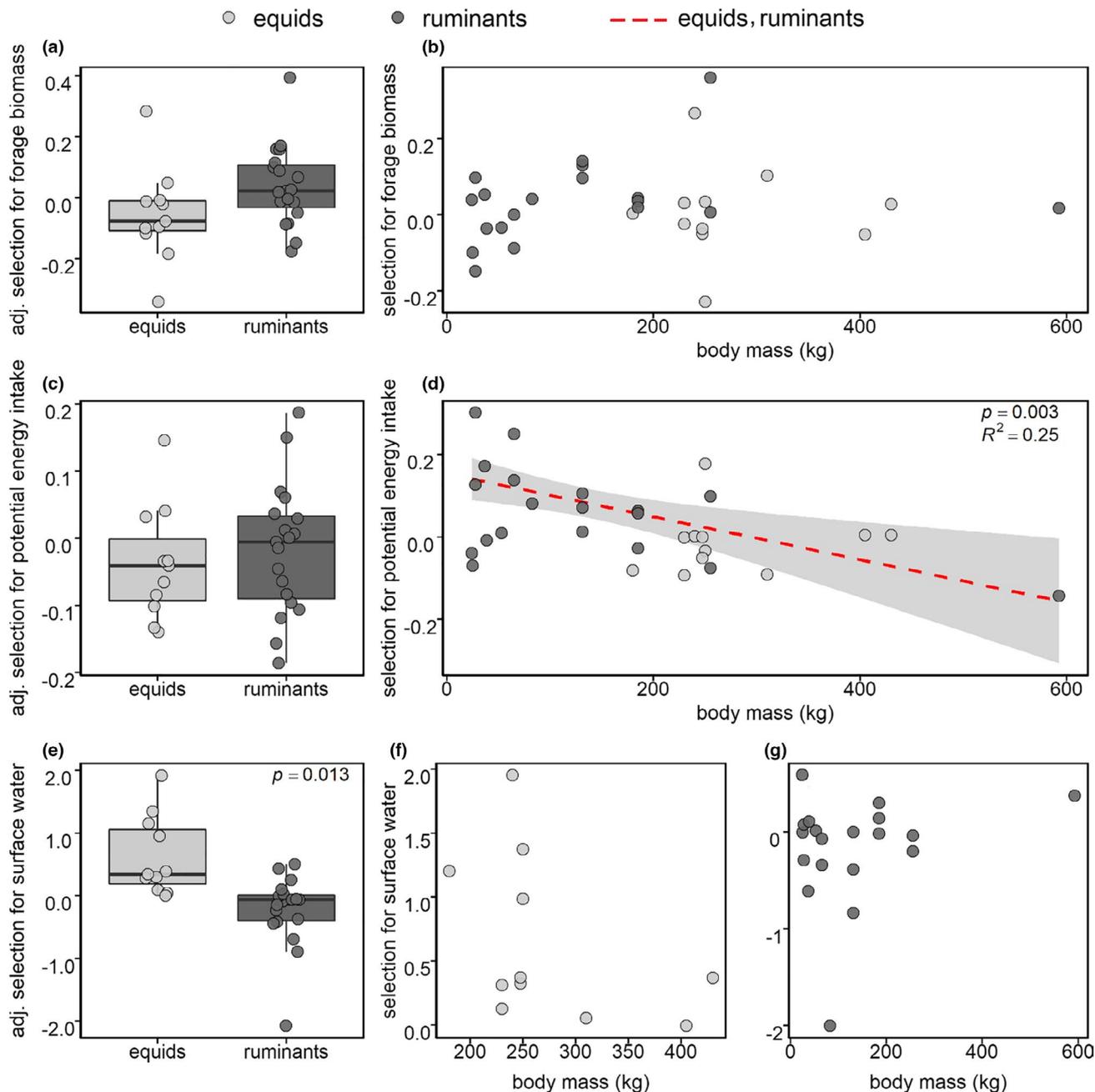
FIGURE 3 Relationship between population-level resource selection coefficients and digestive system (a, c and e; weighted analysis of covariance [ANCOVA]) and body size (b, d, f and g; weighted least squares regression). Equid populations more strongly selected surface water after controlling for the effect of body size (e), but we detected no significant difference in selection for forage biomass (a) and potential energy intake (c) after controlling for the effect of body size differences between equids and ruminants. The effect of body size on selection for potential energy intake was statistically significant for all free-ranging ungulates (d; red dashed line). The effect of body size on selection for surface water was not statistically significant for equids (f) or ruminants (g)

phenological confounding should be restricted to ecosystems in which woody plants and grasses co-occur in similar proportions yet exhibit different seasonality (e.g. eastern and southern African savannahs and European forests).

Differences in the strength and consistency of resource selection were likely due in part to the relatively high diversity of ruminants in our study, which incorporated 11 genera exhibiting a >20-fold difference in body

size (from 24 kg roe deer to 590 kg African buffalo) with additional variation in feeding strategies (e.g. unselective grazing, selective browsing and mixed feeding). However, all species of ruminants in our study foraged largely or wholly in the understorey layer or in open rangelands, for which phenological dynamics were captured by our forage biomass metrics. Our results also are consistent with site-specific studies on ungulate assemblages, where multiple ruminants coexist via resource specialisation,

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BODY SIZE AND DIGESTIVE SYSTEM SHAPE RESOURCE SELECTION BY UNGULATES: A CROSS-TAXA TEST OF THE FORAGE MATURATION HYPOTHESIS

and therefore, exhibit a diverse array of resource selection (Kartzinel et al., 2015; Wilmshurst et al., 2000).

In Serengeti National Park, Wilmshurst et al., (2000) documented empirical support for theoretical expectations that resource selection of ruminants should be mediated by body size. As phenology progresses, increasing forage biomass goes hand-in-hand with decreasing digestibility, presenting a challenge for smaller-bodied herbivores for which small guts filled with slowly fermenting vegetation reduce intake rates (Figure 1; see also Wickstrom et al., 1984). As a result, smaller-bodied ruminants were observed on patches of lower biomass than their larger counterparts. Our findings extend those of Wilmshurst et al., (2000) across four continents, and by incorporating hindgut fermenters. Hindgut fermenters were represented exclusively by equids in our study, which, in contrast to ruminants, are restricted to a single genus (*Equus*) and exhibit limited (~2.5-fold) variation in body size. Consequently, resource selection was relatively consistent across equid populations, with 6 of 11 populations selecting areas in close proximity to surface water. Equids do not conserve water as efficiently as ruminants, and they excrete proportionately more water (Janis, 1976; Ogutu et al., 2014); such differences in digestion likely explain the strong selection for surface water by equids across the globe.

Our remotely sensed imagery of surface water existed at a coarser temporal resolution compared to our remotely sensed imagery of vegetation indices, and did not comprise exhaustive data on all sources of water available to study populations. For example, ephemeral ponds and streams are not captured by the Global Surface Water Explorer. However, with a resolution of 30 x 30 m, the Global Surface Water Explorer constitutes (by far) the most precise data on the global distribution of surface water (Pekel et al., 2016), and we were able to supplement this remotely sensed imagery with locally collected locations of surface water. The strength of selection for surface water did not depend on availability of surface water within study areas (but it did depend on variability in the distance to surface water [Figure S2]) and, as per our initial prediction based on digestive system, the strength of selection for surface water was significantly stronger for equids than for ruminants. In sum, we believe that such methodological limitations associated with remotely sensed imagery of surface water were unlikely to have had undue influence on our results and associated inferences (but see Text S2). More generally, we believe that the Global Surface Water Explorer has strong potential as a tool for wildlife and movement ecologists, and its potential methodological limitations will be overridden by its value in many study systems.

Our study represents a macroecological test of drivers of ungulate resource selection across the globe. By necessity, our synthetic approach sacrifices some area- and population-specific precision in an attempt to identify general trends (Brown, 1995; Levin, 1992). For example,

our use of body size as a predictor variable integrates a suite of size-dependent relationships, including retention time in the digestive tract and cropping rate. In particular, variation in cropping rates among species has potential to influence resource selection: for a given body size, a narrower-muzzled species could more efficiently forage on low biomass compared to a wider-muzzled species (Spalinger & Hobbs, 1992). As another example, all ruminant populations in our study were sympatric with other wild and domestic ruminants, which could influence resource selection of free-ranging ungulates (e.g. Kinnaird & O'Brien, 2012; Mishra et al., 2004). Future efforts to synthesise patterns of resource selection for free-ranging ungulates might incorporate the occurrence and abundance of livestock and population density of the focal species (through, e.g. the Gridded Livestock of the World mapping project by the United Nations). Through resource competition, barriers to movement (e.g. fences and roads) and direct interference, humans can suppress the potential for free-ranging ungulates to exploit spatio-temporal variability in forage biomass, potential energy intake and access to surface water (e.g. Sanderson et al., 2002; Ogutu et al., 2014; Panzacchi et al., 2015; Tucker et al., 2018; but see Young et al., 2018). By constraining movements of free-ranging ungulates, human activity may dampen any effects of body size and digestive system on resource selection and result in deviations from the central prediction of the FMH. Moreover, individual characteristics such as sex, age, body mass and reproductive status of individuals strongly affect energy requirements and, thus, resource selection by large ungulates (e.g. Brivio et al., 2014; Forsyth et al., 2005; Hamel & Côté, 2008; Saïd et al., 2009). Additionally, physical constraints inherent to different study areas (e.g. the spatial scale over which variation in forage biomass and potential energy intake arise) likely influence the movement and resource selection of free-ranging ungulates to some degree (Aikens et al., 2020). Such area- and population-specific variability almost certainly contributes to differences in resource selection between populations of the same species (e.g. khulan populations in western vs. southern Mongolia; Text S2), and could explain variation around the general trends depicted in Figures 2 and 3. Finally, future studies could benefit from separating different movement states (e.g. foraging, resting and travelling) to explicitly investigate resource selection during foraging bouts (Fryxell et al., 2008; Gurarie et al., 2009). Nevertheless, our analyses point to important generalities – stronger selection for surface water by equids relative to ruminants, and stronger selection for potential energy intake by smaller-bodied ruminants – which conform to expectations based on metabolic allometry and digestive system. In combination with intensive, longitudinal field observations within each study population, we believe that our comparative cross-taxa study has helped illuminate general rules and contingencies associated with the FMH.

Our synthetic approach provides the first cross-taxa test of the forage maturation hypothesis. By using a combination of remotely sensed data to quantify forage biomass, potential energy intake and surface water, we assessed differential selection of resources by free-ranging ungulates across the terrestrial surface. In doing so, we have refined the forage maturation hypothesis relative to its original formulation to explicitly consider variation in ungulate body size and digestive system, thus extending the applicability of this key concept in large herbivore ecology. The forage characteristics that influence population persistence of free-ranging ungulates should differ according to body size and digestive system, such that access to a combination of resource gradients is key to maintaining viable populations of diverse free-ranging ungulates across the globe.

DATA AVAILABILITY STATEMENT
The dataset used in our analyses is available via Dryad repository (https://doi.org/10.5061/dryad.jsxksn09f) following a year-long embargo from publication of the manuscript. The coordinates associated with mountain zebra data are not provided in an effort to protect critically endangered black rhino (*Diceros bicornis*) locations. Interested researchers can contact the data owner (Minnesota Zoo) directly for inquiries.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.