Body size and digestive system shape resource selection by ungulates: a cross-taxa test of the Forage Maturation Hypothesis

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Abstract

The Forage Maturation Hypothesis (FMH) states that energy intake for ungulates is maximized 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 generalizable, 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.

Introduction

Animal movements should be influenced by the need to maintain a positive balance between energetic gains and losses (Senft *et al.* 1987; Nathan *et al.* 2008; Owen-Smith *et al.* 2010; Middleton *et al.* 2013). Foraging behaviors employed by ungulates vary according to body size and digestive system (ruminant versus hindgut fermenters; Bell 1971; Demment & Van Soest 1985; Olff *et al.* 2002; Hopcraft *et al.* 2012). 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 (Jarman 1974; McNab 1974; Illius & Gordon 1992; Barboza & Bowyer 2000). Consequently, body size creates trade-offs in how ungulates should prioritize forage biomass and forage digestibility (Bailey *et al.* 1996; Wilmshurst *et al.* 2000; Olff *et al.* 2002).

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 fiber 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 (Spalinger & Hobbs 1992; Wilmshurst *et al.* 2000; Hebblewhite *et al.* 2008). 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 maximized for ungulates at intermediate phenological stages (i.e., when rates of both forage intake and digestibility are at intermediate levels; Fig 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, mixed feeding; Hofmann 1989; Albon & Langvatn 1992; Mueller *et al.* 2008; Middleton *et al.* 2018). As a result, the FMH frequently forms the basis for conceptualizing 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 maximize 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, per unit time) are higher for smaller ungulates, while absolute requirements (i.e., energy and protein per individual, 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 (Fig. 1A, Fig. 1B).

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; Santos *et al.* 2011; Owens & Basalan 2016). In contrast, hindgut fermenters have reduced retention time, but lower rates of protein extraction (Janis 1976; Duncan *et al.* 1990; 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 favor ungulate movements that optimize 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; Fig. 1B, 1C).

We tested the central prediction of the FMH by linking high-resolution movement trajectories (unavailable when the FMH was conceptualized) 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 maximize energy intake, thereby conforming to the central prediction of the FMH (Fig. 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 (Fig. 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 data set of GPS locations for 11 populations of equids and 19 populations of ruminants totaling 580 individuals; data for all study populations were collected between 2005 and 2019 (Figure 2A; Table S1). The equid data set comprised GPS relocations for seven (out 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 data set 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 coauthors or by excluding locations with dilution of precision > 10.

We restricted our analyses to habitats with minimal canopy cover, including rangelands, savannas, 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% "dense forest", as classified by the Food and Agriculture Organization (FAO; Friedl & Sulla-Menashe 2015). The second criterion required that percent (%) tree cover across the entire study area was <40% (Hansen *et al.* 2013; Table S1). We calculated percent 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 meters and temporal resolution of a year (Friedl & Sulla-Menashe 2015) and Global 2010 Tree Cover (spatial resolution 30 meters, 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 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 x 250 m, temporal resolution eight days) using the MSAVI2 method and equations described in Qi *et al.* (1994) as a proxy of forage biomass (Pettorelli *et al.* 2005; Borowik *et al.* 2013). In arid environments, MSAVI and other soil-adjusted indices of vegetation are more appropriate than the more commonly used Normalized Difference Vegetation Index (NDVI) because they minimize 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 categorized 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, Bischof et al. 2012; Avgar et *al.* 2013; Geremia *et al.* 2019). The IRG is positively correlated with the peak in fecal 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 (Merkle *et al.* 2016; Rivrud *et al.* 2016; Branco *et al.* 2019); 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 Fig. 1A). We therefore used both IRG and MSAVI to disentangle selection for potential energy intake and forage biomass. We normalized 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; Merkle *et al.* 2016; Branco *et al.* 2019).

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-normalized) MSAVI and IRG values associated with each of the random points, and plotting annual MSAVI and IRG profiles (Fig. S1). For study areas with a single “growing season” per year (25 out 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 (Fig. 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 (Fig. S1B). We then filtered our data set 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 due to computational restrictions (Redfern *et al.* 2003; Pekel *et al.* 2016; Huang *et al.* 2018). Further, 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 one 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 x 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 normalized 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 (Thurfjell *et al.* 2014; Avgar *et al.* 2016) 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; Fleming *et al.* 2014; Dupke *et al.* 2017). 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), then compared observed and potential steps using conditional logistic regression (Fortin *et al.* 2005). In addition to step length (standardized 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 (Roever *et al.* 2010; Merkle *et al.* 2016; Prima *et al.* 2017). 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. Further, 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), nor 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 (Merkle *et al.* 2016; Aikens *et al.* 2017). 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 (Therneau & Lumley 2015; R Core Team 2019; Signer *et al.* 2019).

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., exhibit functional responses in habitat selection [Mysterud and Ims 1998; Holbrook *et al.* 2019]), 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; Fig. 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 for 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 out of 30 equid and ruminant populations (Fig. 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 out of 11 equid populations (55%) selected for surface water, with 10 out of 11 equid populations (91%) having a positive parameter estimates for surface water (Fig. 2). Ruminant populations displayed a diversity of selection behaviors toward surface water. Overall, equids consistently selected for surface water, while resource selection of ruminants was variable (Fig. 2).

After controlling for the effect of body size, we did not detect any difference in selection for forage biomass ($P = 0.18$; Fig. 3A) or potential energy intake ($P = 0.37$; Fig. 3C) between equids and ruminants. Body size did not explain variation in selection for forage biomass (Fig. 3B) but did explained 25% of the variation in selection for potential energy intake (Fig. 3D). Equids selected for surface water more strongly than ruminants after controlling for the effect of body size ($F_{(1, 27)} = 7.09$, $P = 0.013$; Fig. 3E). Body size did not explain selection for surface water in equids and ruminants ($P \geq 0.23$; Fig. 3F and 3G).

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 (Illius & Gordon 1987; Hopcraft *et al.* 2012). 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 prioritize 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., Wilmshurst *et al.* 2000, Hebblewhite *et al.* 2008, Geremia *et al.* 2019). 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 between forage biomass, forage quality, and remotely-sensed metrics directly (e.g., Hebblewhite *et al.* 2008, Wilmers *et al.* 2013, Geremia *et al.* 2019), 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 standardized 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 minimize 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 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 savannas 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, mixed feeding). However, all species of ruminants in our study foraged largely or wholly in the understory 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 specialization, and therefore exhibit a diverse array of resource selection (Wilmshurst *et al.* 2000; Kartzinel *et al.* 2015).

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 reduces intake rates (Fig. 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 six 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 [Fig. S2]) and, 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 attempt to identify general trends (Levin 1992, Brown 1995). 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 and 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., Mishra *et al.* 2004; Kinnaird & O’Brien 2012). Future efforts to synthesize 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, creating barriers to movement (e.g., fences, roads), and direct interference, humans can suppress the potential for free-ranging ungulates to exploit spatiotemporal 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., Forsyth *et al.* 2005; Hamel & Côté 2008; Saïd *et al.* 2009; Brivio *et al.* 2014). 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 versus 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, 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 of 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.

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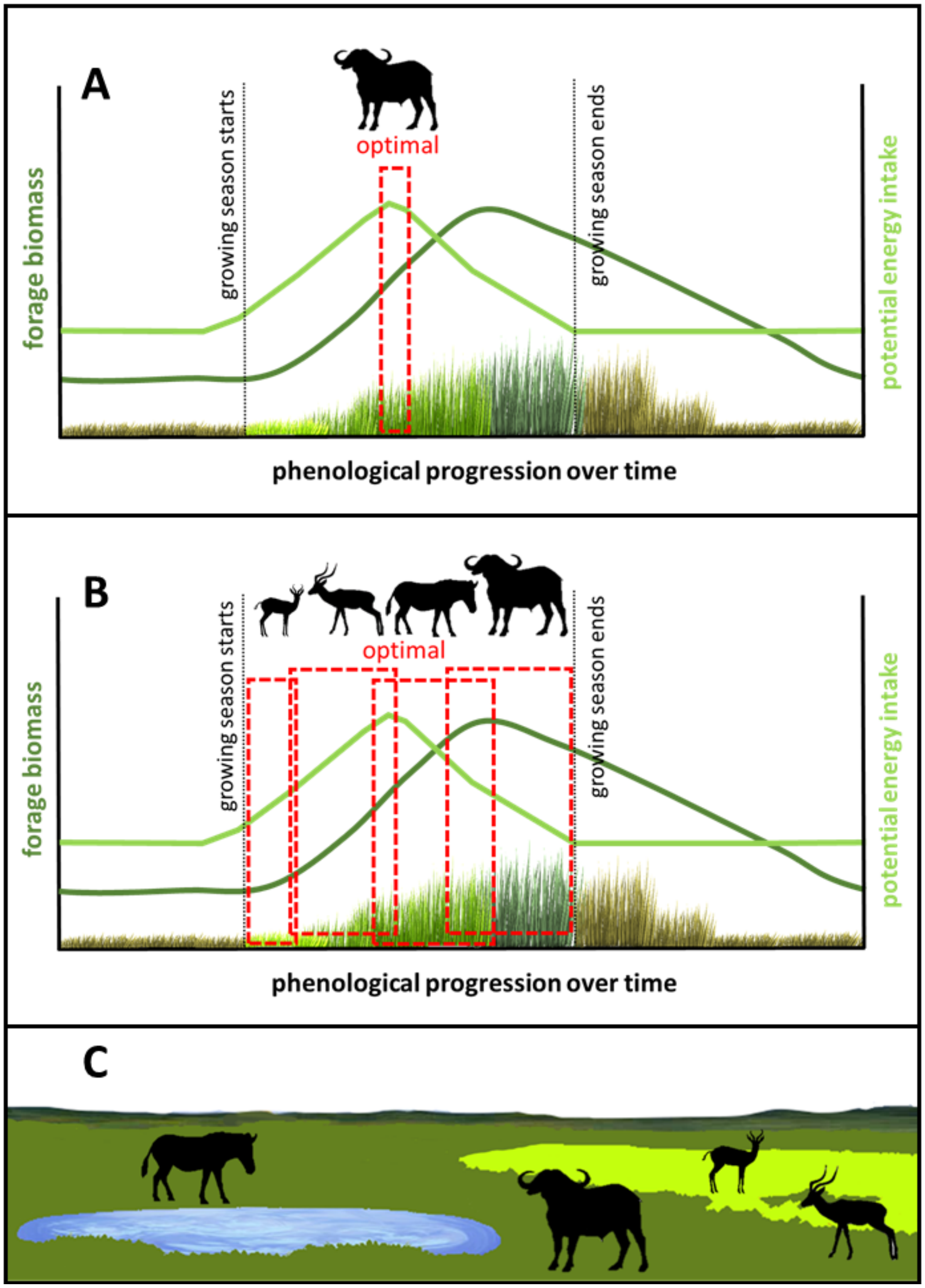
Figures

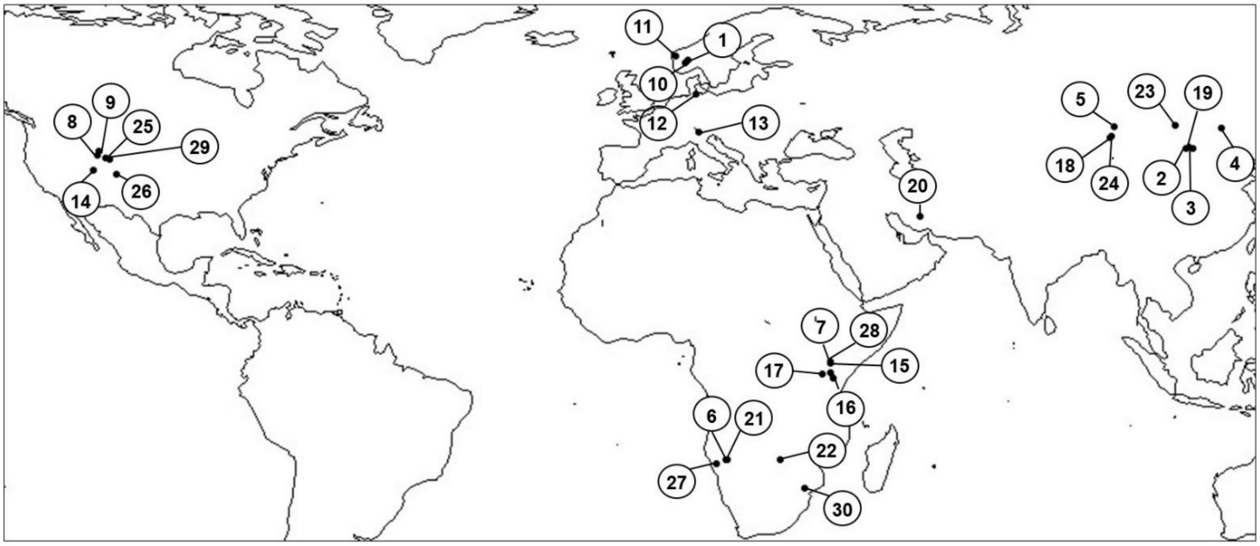
Figure 1. Illustrated predictions for resource selection by equids and different sizes of ruminants during a hypothetical growing season and in a hypothetical landscape. Forage biomass (dark green line) and potential energy intake (light green line; measured by rate of change in forage biomass) increase 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 maximize 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.

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).

Figure 3. Relationship between population-level resource selection coefficients and digestive system (A, C, E; weighted analysis of covariance [ANCOVA]) and body size (B, D, F, 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) nor for ruminants (G).


A
growing season starts
optimal
growing season ends
forage biomass
potential energy intake
phenological progression over time
B
growing season starts
optimal
growing season ends
forage biomass
potential energy intake
phenological progression over time
C


11
1
10
12
13
9
8
25
29
14
26
5
23
19
18
24
2
3
4
20
7
28
17
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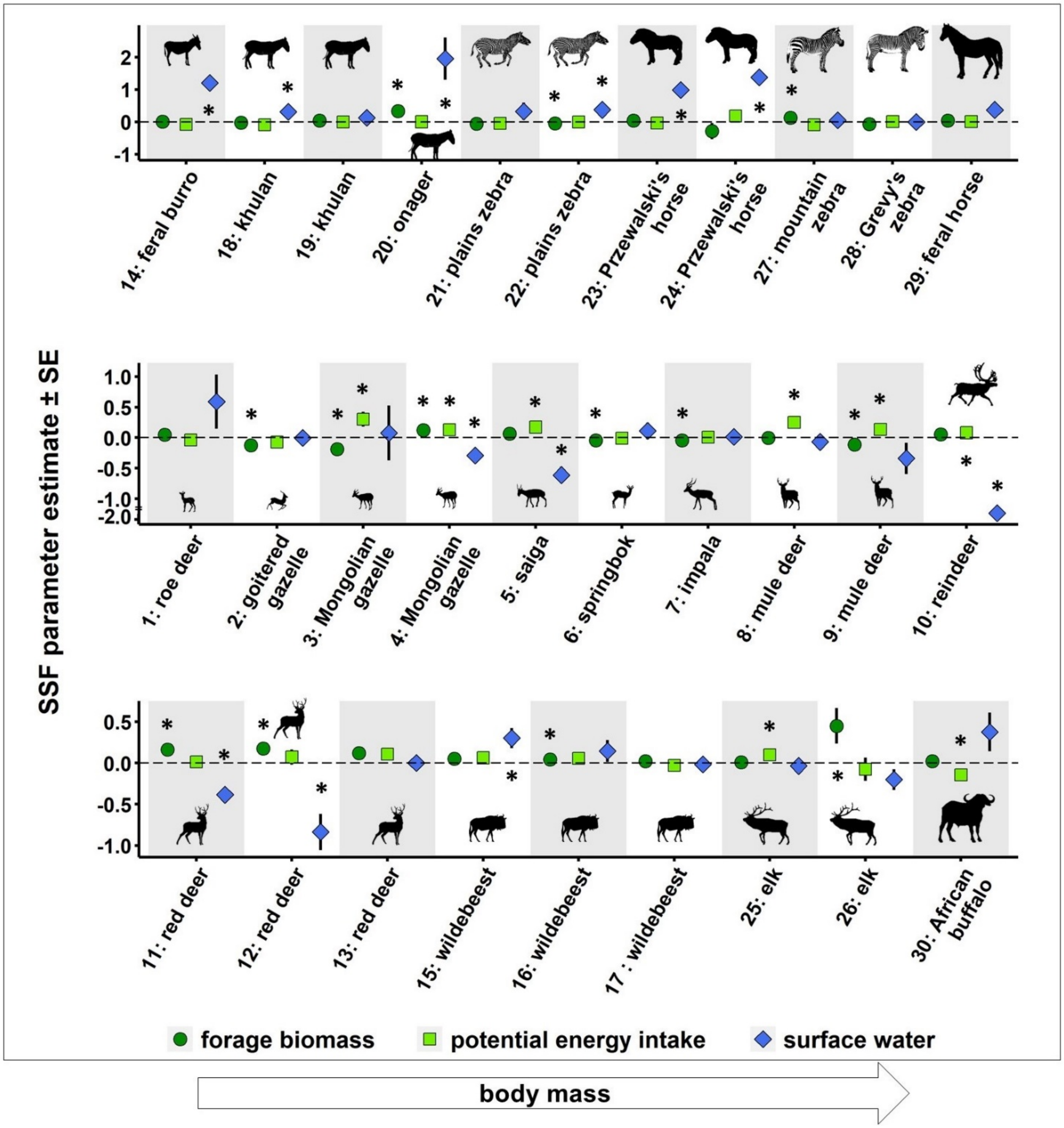
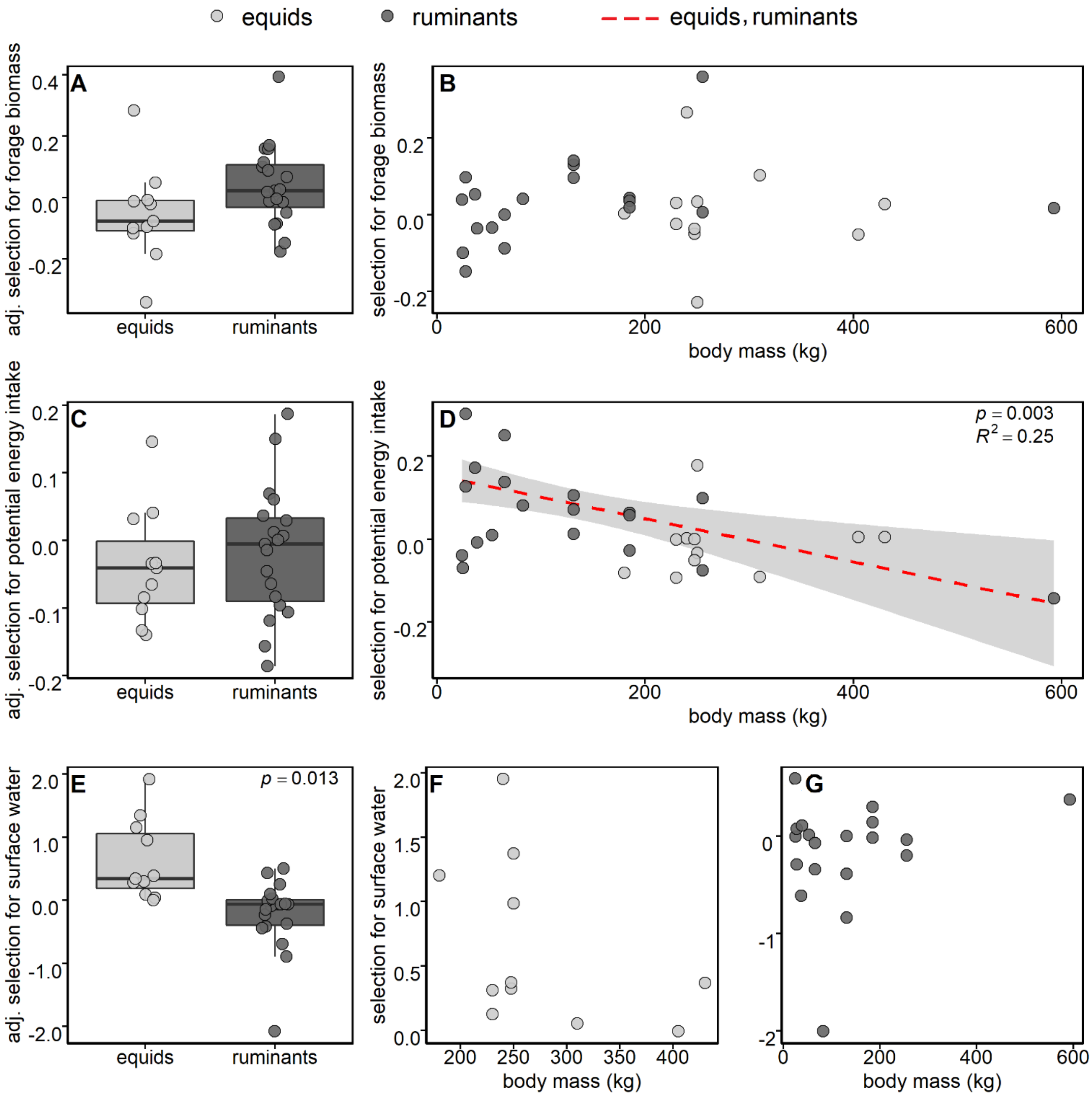
16
6
21
22
27
30


SSF parameter estimate ± SE
2
1
0
-1
14: feral burro
18: khulan
19: khulan
20: onager
21: plains zebra
22: plains zebra
23: Przewalski's horse
24: Przewalski's horse
27: mountain zebra
28: Grevy's zebra
29: feral horse
1.0
0.5
0.0
-0.5
-1.0
-2.0
1: roe deer
2: goitered gazelle
3: Mongolian gazelle
4: Mongolian gazelle
5: saiga
6: springbok
7: impala
8: mule deer
9: mule deer
10: reindeer
0.5
0.0
-0.5
-1.0
11: red deer
12: red deer
13: red deer
15: wildebeest
16: wildebeest
17 : wildebeest
25: elk
26: elk
30: African buffalo
*
● forage biomass
■ potential energy intake
◆ surface water
body mass


equids
ruminants
equids, ruminants
A
adj. selection for forage biomass
0.4
0.2
0.0
-0.2
equids
ruminants
B
selection for forage biomass
0.2
0.0
-0.2
0
200
400
600
body mass (kg)
C
adj. selection for potential energy intake
0.2
0.1
0.0
-0.1
-0.2
equids
ruminants
D
$p = 0.003$
$R^2 = 0.25$
selection for potential energy intake
0.2
0.0
-0.2
0
200
400
600
body mass (kg)
E
$p = 0.013$
adj. selection for surface water
2.0
1.0
0.0
-1.0
-2.0
equids
ruminants
F
selection for surface water
2.0
1.5
1.0
0.5
0.0
200
250
300
350
400
body mass (kg)
G
0
-1
-2
0
200
400
600
body mass (kg)