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

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79 compiled, managed, and analyzed the data (and collected GPS locations for onagers in southern  
80 Iran), and drafted the manuscript. BRJ, SEA, and EOA provided analytical assistance, and BRJ  
81 provided feedback on the methods. JRG and BRJ revised the drafts. All coauthors collected data,  
82 contributed to revisions, and gave final approval for publication.

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85 contact owners of the datasets for requests.

## 86 **Abstract**

87 The Forage Maturation Hypothesis (FMH) states that energy intake for ungulates is maximized  
88 when forage biomass is at intermediate levels. Nevertheless, metabolic allometry and different  
89 digestive systems suggest that resource selection should vary across ungulate species. By  
90 combining GPS relocations with remotely-sensed data on forage characteristics and surface  
91 water, we quantified the effect of body size and digestive system in determining movements of  
92 30 populations of hindgut fermenters (equids) and ruminants across biomes. Selection for  
93 intermediate forage biomass was negatively related to body size, regardless of digestive system.  
94 Selection for proximity to surface water was stronger for equids relative to ruminants, regardless  
95 of body size. To be more generalizable, we suggest that the FMH explicitly incorporate  
96 contingencies in body size and digestive system, with small-bodied ruminants selecting more  
97 strongly for potential energy intake, and hindgut fermenters selecting more strongly for surface  
98 water.

99 **Introduction**

100 Animal movements should be influenced by the need to maintain a positive balance between  
101 energetic gains and losses (Senft *et al.* 1987; Nathan *et al.* 2008; Owen-Smith *et al.* 2010;  
102 Middleton *et al.* 2013). Foraging behaviors employed by ungulates vary according to body size  
103 and digestive system (ruminant versus hindgut fermenters; Bell 1971; Demment & Van Soest  
104 1985; Olf *et al.* 2002; Hopcraft *et al.* 2012). Smaller-bodied ungulates (i.e., ruminants,  
105 primarily) should forage in patches with highly digestible forage (high energy and nutrient  
106 concentrations) because they possess high mass-specific metabolic rates. In contrast, larger-  
107 bodied ungulates (i.e., both larger-bodied ruminants and hindgut fermenters) should forage in  
108 high biomass patches because of higher absolute energy demands (Jarman 1974; McNab 1974;  
109 Illius & Gordon 1992; Barboza & Bowyer 2000). Consequently, body size creates trade-offs in  
110 how ungulates should prioritize forage biomass and forage digestibility (Bailey *et al.* 1996;  
111 Wilmshurst *et al.* 2000; Olf *et al.* 2002).

112 For nearly 30 years, the Forage Maturation Hypothesis (hereafter “FMH”; Fryxell 1991)  
113 has provided a lens for understanding resource selection and movements of free-ranging  
114 ungulates (Fryxell 1991; Hebblewhite *et al.* 2008; Merkle *et al.* 2016). Digestibility of forage is  
115 highest at the beginning of the growing season because plants lack structural fiber needed to  
116 support high biomass (Van Soest 1996). At this earliest phenological stage, however, plants are  
117 small and biomass is limiting, so energy intake of ungulates may be limited by bite size  
118 (Spalinger & Hobbs 1992; Wilmshurst *et al.* 2000; Hebblewhite *et al.* 2008). Digestibility then  
119 declines as plants mature, gain biomass, and become more fibrous (Van Soest 1996). Because of  
120 this phenological trade-off between biomass and digestibility of plants, and according to the  
121 FMH, energy intake is maximized for ungulates at intermediate phenological stages (i.e., when

122 rates of both forage intake and digestibility are at intermediate levels; Fig 1A). Although the  
123 FMH was originally developed to explain resource selection in tropical, bulk-grazing ruminants,  
124 its predictions are relevant for temperate ruminants that display a diversity of feeding strategies  
125 (e.g., unselective grazing, selective browsing, mixed feeding; Hofmann 1989; Albon & Langvatn  
126 1992; Mueller *et al.* 2008; Middleton *et al.* 2018). As a result, the FMH frequently forms the  
127 basis for conceptualizing resource selection and movements of ungulates—including large- and  
128 small-bodied species, and hindgut and ruminant fermenters—across the globe (e.g., Drescher *et*  
129 *al.* 2006; Edouard *et al.* 2010; Fleurance *et al.* 2010; St-Louis & Cote 2014).

130         The central prediction of the FMH—that ungulates should select forage of intermediate  
131 biomass and intermediate digestibility to maximize energy intake—should hinge largely on body  
132 size. In 1971, Bell first articulated how metabolic rate should interact with resource selection by  
133 free-ranging ungulates, stating that relative requirements (i.e., energy and protein per unit  
134 weight, per unit time) are higher for smaller ungulates, while absolute requirements (i.e., energy  
135 and protein per individual, per unit time) are higher for larger ungulates (Bell 1971). Over two  
136 decades ago, Wilmshurst *et al.* (2000) extended the work of Bell (1971) and Fryxell (1991) by  
137 testing quantitative predictions for selection of optimal biomass by five co-occurring ruminants  
138 in Serengeti National Park. Wilmshurst *et al.* (2000) predicted that optimal biomass of plants  
139 selected by large herbivores would vary as a function of body size, at least among ruminants.  
140 Specifically, resource selection should occur along a gradient from high digestibility/low  
141 biomass to low digestibility/high biomass, dependent on body size. Explicitly considering and  
142 testing for this contingency among a diversity of ungulates would refine the predictive capacity  
143 of the FMH, thereby advancing its application to ungulates more generally (Fig. 1A, Fig. 1B).

144 In addition to forage biomass and energy content, reliance on surface water restricts the  
145 movement and distribution of ungulates across some landscapes (Rozen-Rechels *et al.* 2019;  
146 Veldhuis *et al.* 2019). Ruminants efficiently extract protein from fresh plant tissue because the  
147 fermentation site (rumen) occurs anterior to the absorption site (small intestine) for proteins.  
148 Ruminants therefore employ an “efficient” urea cycle in which available nitrogen is recycled  
149 throughout the digestive tract, thereby conserving water (Janis 1976; Santos *et al.* 2011; Owens  
150 & Basalan 2016). In contrast, hindgut fermenters have reduced retention time, but lower rates of  
151 protein extraction (Janis 1976; Duncan *et al.* 1990; Van Soest 1996). Consequently, hindgut  
152 fermenters excrete more urea, which must be accompanied by water. Larger-bodied ungulates—  
153 and larger-bodied hindgut fermenters in particular—consume large amounts of biomass and  
154 should therefore be further tied to surface water (i.e., water available for drinking, as opposed to  
155 contained within plants) because high-biomass forage tends to be drier (Bell 1971; Redfern *et al.*  
156 2003; Schoenecker *et al.* 2016). Therefore, constraints associated with conserving water in the  
157 body should tie hindgut fermenters to water, and potentially result in deviations from the central  
158 prediction of the FMH (which is based purely on biomass and digestibility of forage). In sum,  
159 natural selection should favor ungulate movements that optimize net energy gain despite  
160 constraints imposed by forage biomass, the energy contained within forage, and surface water,  
161 with the relative importance of each arising as a function of body size and digestive system  
162 (Redfern *et al.* 2003; Fig. 1B, 1C).

163 We tested the central prediction of the FMH by linking high-resolution movement  
164 trajectories (unavailable when the FMH was conceptualized) with selection of forage biomass,  
165 potential energy intake, and surface water by free-ranging ungulates. We evaluated the relative  
166 influence of body size and digestive system on selection for these resources by ruminants

167 (foregut fermenters) and equids (Family Equidae, representing hindgut fermenters) using GPS  
168 telemetry data from 30 populations of 19 species distributed across the biomes. We predicted  
169 that (1) smaller-bodied ungulates (all of which exhibit ruminant fermentation) would select for  
170 resource patches that maximize energy intake, thereby conforming to the central prediction of the  
171 FMH (Fig. 1A); whereas (2) by virtue of their larger body size, resource selection patterns of  
172 both larger-bodied ruminants and equids would deviate from this prediction (Fig. 1B).  
173 Specifically, we expected that larger-bodied ruminants would select most strongly for patches of  
174 high forage biomass, whereas equids (because of their hindgut fermentation) would select most  
175 strongly for patches close to water.

## 176 **Methods**

### 177 *Data Collection*

178 We compiled a global data set of GPS locations for 11 populations of equids and 19 populations  
179 of ruminants totaling 580 individuals; data for all study populations were collected between 2005  
180 and 2019 (Figure 2A; Table S1). The equid data set comprised GPS relocations for seven (out of  
181 nine) extant species of wild and feral equids: Asiatic wild ass (khulan, *Equus hemionus hemionus*  
182 and onager, *E. h. onager*), feral burro (*E. asinus*), feral horse (*E. caballus*), Grevy's zebra (*E.*  
183 *grevyi*), mountain zebra (*E. zebra*), plains zebra (*E. quagga*), and Przewalski's horse (*E. ferus*).  
184 The ruminant data set included GPS relocations for 12 species: African buffalo (*Syncerus caffer*),  
185 elk (*Cervus canadensis*), goitered gazelle (*Gazella subgutturosa*), impala (*Aepyceros melampus*),  
186 Mongolian gazelle (*Procapra gutturosa*), mule deer (*Odocoileus hemionus*), red deer (*Cervus*  
187 *elaphus*), reindeer (*Rangifer tarandus tarandus*), roe deer (*Capreolus capreolus*), saiga antelope  
188 (*Saiga tatarica*), springbok (*Antidorcas marsupialis*), and white-bearded wildebeest



189 (*Connochaetes taurinus*). Equid species ranged in body size from 180 kg (feral burro) to 430 kg  
190 (feral horse; Wilson & Mittermeier 2011); ruminant species ranged in body size from 24 kg (roe  
191 deer) to 592 kg (African buffalo; Wilson & Mittermeier 2011). Hereafter, we distinguish  
192 between “study areas” (the geographic locales in which resource selection were quantified) and  
193 “study populations” (individuals fitted with GPS collars within a study area; Table S1). Five of  
194 our study areas contained multiple study populations, and eight species were represented by two  
195 or more study populations spread across different study areas (Table S1). Inaccurate GPS  
196 locations were removed either by coauthors or by excluding locations with dilution of precision  
197 > 10.

198         We restricted our analyses to habitats with minimal canopy cover, including rangelands,  
199 savannas, open forest, and tundra. We intended to include sufficiently open canopies for  
200 remotely-sensed vegetation indices to work properly. Therefore, we applied two criteria in  
201 selecting study populations. The first criterion required that a study area be comprised of <20%  
202 “dense forest”, as classified by the Food and Agriculture Organization (FAO; Friedl & Sulla-  
203 Menashe 2015). The second criterion required that percent (%) tree cover across the entire study  
204 area was <40% (Hansen *et al.* 2013; Table S1). We calculated percent of the study area covered  
205 with dense forest and mean % tree cover within minimum convex polygons (MCP) constructed  
206 for each study population using the Terra and Aqua combined Moderate Resolution Imaging  
207 Spectroradiometer (MODIS) Land Cover Type, MCD12Q1, Version 6, layer 7, spatial resolution  
208 of 500 meters and temporal resolution of a year (Friedl & Sulla-Menashe 2015) and Global 2010  
209 Tree Cover (spatial resolution 30 meters, Hansen *et al.* 2013), respectively.

210 *Forage Biomass and Potential Energy Intake*

211 To delineate study areas, we computed the MCP around each population's GPS locations and  
212 buffered the MCP by 5 km to ensure that we captured adjacent habitats that were available to  
213 telemetered individuals. Within each study area, we extracted Modified Soil-Adjusted  
214 Vegetation Index (MSAVI; MODIS terra satellite imagery Version 6.0 MOD09Q1; spatial  
215 resolution 250 x 250 m, temporal resolution eight days) using the MSAVI2 method and  
216 equations described in Qi *et al.* (1994) as a proxy of forage biomass (Pettorelli *et al.* 2005;  
217 Borowik *et al.* 2013). In arid environments, MSAVI and other soil-adjusted indices of vegetation  
218 are more appropriate than the more commonly used Normalized Difference Vegetation Index  
219 (NDVI) because they minimize the influence of bare ground on estimates of vegetation (Qi *et al.*  
220 1994). Additionally, NDVI and MSAVI are extracted from similar spectral bands, and usually  
221 are strongly correlated in temperate conditions (Jin *et al.* 2014; Liang *et al.* 2016). We removed  
222 pixels categorized as snow, cloud, or shadow using quality assessment bands, then smoothed  
223 each time-series of MSAVI using a moving three-scene median filter and applied a linear  
224 interpolation (Branco *et al.* 2019).

225 To estimate the instantaneous rate of green-up (IRG), we calculated the rate of change in  
226 MSAVI for every three consecutive dates by using a three-scene moving window (Avgar *et al.*  
227 2013; Branco *et al.* 2019). The IRG is a metric that combines both forage biomass and forage  
228 digestibility, which collectively equate to potential energy intake (i.e., a proxy of energy that  
229 could be effectively available to the feeder, Bischof *et al.* 2012; Avgar *et al.* 2013; Geremia *et al.*  
230 2019). The IRG is positively correlated with the peak in fecal crude protein in ungulates (Hamel  
231 *et al.* 2009) and has been used widely as an index of the energy contained in forage across space  
232 and time (Merkle *et al.* 2016; Rivrud *et al.* 2016; Branco *et al.* 2019); days from peak IRG is  
233 strongly correlated with N:C ratios in grasses (Geremia *et al.* 2019). Hereafter, we refer to

234 selection for IRG as selection for “potential energy intake”. Similarly, and hereafter, we refer to  
235 selection for peak biomass of forage as simply selection for “forage biomass”. Although IRG  
236 combines both forage biomass and forage digestibility, it is not redundant with metrics that  
237 solely represent forage biomass: while high IRG values represent intermediate plant biomass,  
238 low values of IRG may represent either low or high biomass (see Fig. 1A). We therefore used  
239 both IRG and MSAVI to disentangle selection for potential energy intake and forage biomass.  
240 We normalized both MSAVI and IRG values between 0 and 1 based on the lowest and highest  
241 value of each pixel in a year, respectively. Thus, for each pixel, an MSAVI value of 1  
242 represented the highest biomass and a value of 0 represented the lowest biomass in a given year,  
243 for a given study population. Similarly, an IRG value of 1 represents forage at a state of  
244 intermediate biomass (and the peak rate of green-up), whereas an IRG value of 0 represents  
245 forage at a low rate of change. Collectively, these two layers therefore represent metrics of plant  
246 phenology across space and time (see also Bischof *et al.* 2012; Merkle *et al.* 2016; Branco *et al.*  
247 2019).

248         To evaluate how body size and digestive system influenced resource selection, we  
249 temporally constrained our analysis times when plants were actively growing (to ensure positive  
250 IRG was available to the animals). We determined the duration of growing seasons in each study  
251 population by randomly generating 10,000 points within each study area, extracting absolute  
252 (non-normalized) MSAVI and IRG values associated with each of the random points, and  
253 plotting annual MSAVI and IRG profiles (Fig. S1). For study areas with a single “growing  
254 season” per year (25 out of 30 study populations), we defined the beginning of the “growing  
255 season” as the Julian day when IRG became positive for three consecutive scenes, and the end of  
256 the “growing season” as the Julian day when IRG reached the minimum negative point, followed

257 by IRG values less than or equal to zero (Fig. S1A; *sensu* Jesmer *et al.* 2018). For study areas  
258 with multiple growing seasons per year, we attempted to define each “growing season”  
259 consistent with the method described above (Fig. S1B). We then filtered our data set to only  
260 those relocations that occurred during growing seasons (Table S1).

### 261 *Distance to Surface Water*

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

268 *1-Remotely-sensed data on surface water:* we used monthly data from the Global Surface  
269 Water Explorer (Pekel *et al.* 2016) to estimate occurrence of surface water during the growing  
270 season for each study area. With a spatial resolution of 30 x 30 m and temporal resolution of one  
271 month, the Global Surface Water Explorer constitutes the most precise data on the distribution of  
272 surface water (Pekel *et al.* 2016). For each study area and growing season, we extracted monthly  
273 time series of pixels, where each pixel was assigned a 1 or 0, indicating presence versus absence  
274 of surface water. We then merged monthly layers into a single layer of surface water.

275 *2-Locally-collected data on surface water:* to increase accuracy of our estimates of surface water  
276 for each study population, we compiled data on springs, streams, small ponds, and man-made  
277 water sources (i.e., surface water sources <30 x 30 m that were undetectable using the Global  
278 Water Surface Explorer; Text S1 and Table S2). We merged the locations of locally-collected

279 surface water with the layer on remotely-sensed data on surface water. We then generated a  
280 distance to surface water layer by calculating linear distances between centroids of pixels  
281 classified as “surface water” and centroids of non-surface water pixels. To ensure that our  
282 distance to surface water layer occurred at a comparable scale with MSAVI and IRG, we  
283 normalized values for distance to surface water between 0 and 1 for each study area based on the  
284 lowest and highest value of pixels in each growing season, respectively.

### 285 *Statistical Analyses*

286 We built step-selection functions (Thurfjell *et al.* 2014; Avgar *et al.* 2016) to quantify how  
287 spatiotemporal patterns of forage biomass, potential energy intake, and surface water influenced  
288 movements by ungulates in each study population during growing seasons. To meet the  
289 assumption that the speed of successive steps was uncorrelated (since the step-selection method  
290 assumes Brownian motion), we used the R package CTMM (Calabrese *et al.* 2016) to estimate  
291 the average time at which 99% of the correlation in speed between successive steps had decayed  
292 (i.e., about 3 times of  $\tau V$ ; Fleming *et al.* 2014) in each population. We then rarified (i.e.,  
293 temporally subsampled) the GPS locations of each population, which resulted in uncorrelated,  
294 successive steps (Table S1; Fleming *et al.* 2014; Dupke *et al.* 2017). For each observed (used)  
295 step, we generated 100 potential (unused) steps by fitting a gamma and von Mises distribution to  
296 the step lengths and turning angles, respectively (Signer *et al.* 2019), then compared observed  
297 and potential steps using conditional logistic regression (Fortin *et al.* 2005). In addition to step  
298 length (standardized to a mean of 0.0 and standard deviation of 1.0), we extracted values of  
299 forage biomass, potential energy intake, and distance to surface water at the end points of each  
300 observed and potential step. We used conditional logistic regression to estimate selection

301 coefficients, with each stratum consisting of an observed step and its associated 100 potential  
302 steps, and each individual as an independent cluster in fitting a separate model for each study  
303 population (Roever *et al.* 2010; Merkle *et al.* 2016; Prima *et al.* 2017). Correlation among the  
304 independent variables was minimal (mean  $r$  between MSAVI and IRG = -0.09, range = -0.34 to  
305 0.20; mean  $r$  between MSAVI and distance to surface water = 0.02, range = -0.17 to 0.55; mean  
306  $r$  between IRG and distance to water = 0.008, range = -0.28 to 0.22; Table S3). Since layers for  
307 forage biomass and potential energy intake encompassed both spatial and temporal variation  
308 across landscapes, but surface water layers encompassed only spatial variation across landscapes,  
309 we did not include interactions between forage biomass and water, or between potential energy  
310 intake and water in our analyses. Further, we did not find a significant correlation between  
311 selection for forage biomass and availability of surface water (i.e., mean distance to surface  
312 water; left panel of Figure S3), nor did we find a significant correlation between selection for  
313 potential energy intake and mean distance to surface water (right panel of Figure S3). Sample  
314 sizes (numbers of individuals telemetered, and the range in numbers of individuals telemetered  
315 for a given year) are presented for each study population in Table S1. We interpreted that  
316 significant, positive selection for IRG was indicative of movements consistent with the FMH  
317 (Merkle *et al.* 2016; Aikens *et al.* 2017). We considered variables significant in the models when  
318 95% confidence intervals around parameter estimates did not encompass zero. We performed  
319 these analyses using packages “amt” and “survival” in Program R (Therneau & Lumley 2015; R  
320 Core Team 2019; Signer *et al.* 2019).

321 We next tested the effect of body size and digestive system (i.e., equids or hindgut  
322 fermenters vs. ruminants or foregut fermenters) on resource selection across populations using  
323 weighted least square regressions and analysis of covariance (ANCOVA). Because resource

324 selection may intensify when a particular resource is scarce, variable, or both (i.e., exhibit  
325 functional responses in habitat selection [Mysterud and Ims 1998; Holbrook *et al.* 2019]), we  
326 performed pairwise correlations between population-level selection coefficients for each  
327 resource and the (1) mean value of MSAVI, IRG, and distance to surface water; and (2) the  
328 coefficient of variation (CV) of MSAVI, IRG, and distance to surface water. We did not find  
329 strong support for functional responses in resource selection (i.e., the effect of resource  
330 availability and variability on resource selection; Fig. S2), so we attributed variation in selection  
331 coefficients to some combination of body size and digestive system. For each of the above tests,  
332 we used the parameter estimates derived from the step-selection functions as response variables,  
333 and the number of telemetered individuals in each population as a weighting factor. Second, we  
334 used weighted ANCOVA to control for the effect of body size (i.e., mean species-specific, sex-  
335 unspecific body weight of an adult; Wilson & Mittermeier 2011) in resource selection. When we  
336 did not find a statistically significant effect of digestive system on resource selection after  
337 controlling for body size, we pooled equids and ruminants into weighted regression models to  
338 test how resource selection was influenced by body size. When the effect of digestive system on  
339 resource selection was statistically significant after controlling for body size, we used weighted  
340 regression models with body size as a predictor for equids and for ruminants separately. We  
341 switched the direction of parameter estimates for distance to surface water in all analyses and  
342 graphs. Therefore, positive and negative values show selection and avoidance for forage  
343 biomass, potential energy intake, and surface water, respectively.

## 344 **Results**

345 Forage biomass, potential energy intake, distance to surface water, or some combination thereof  
346 significantly influenced resource selection in 23 out of 30 equid and ruminant populations (Fig.  
347 2; Table S4). Selection for forage biomass was exhibited by two equids (18%) and five  
348 ruminants (26%); avoidance of forage biomass was exhibited by one equid (1%) and five  
349 ruminants (26%). Seven ruminants (37%) and no equids selected for potential energy intake (i.e.,  
350 had movement consistent with the FMH), and one ruminant (0.5%) avoided potential energy  
351 intake. Six out of 11 equid populations (55%) selected for surface water, with 10 out of 11 equid  
352 populations (91%) having a positive parameter estimates for surface water (Fig. 2). Ruminant  
353 populations displayed a diversity of selection behaviors toward surface water. Overall, equids  
354 consistently selected for surface water, while resource selection of ruminants was variable (Fig.  
355 2).

356         After controlling for the effect of body size, we did not detect any difference in selection  
357 for forage biomass ( $P = 0.18$ ; Fig. 3A) or potential energy intake ( $P = 0.37$ ; Fig. 3C) between  
358 equids and ruminants. Body size did not explain variation in selection for forage biomass (Fig.  
359 3B) but did explained 25% of the variation in selection for potential energy intake (Fig. 3D).  
360 Equids selected for surface water more strongly than ruminants after controlling for the effect of  
361 body size ( $F_{(1, 27)} = 7.09$ ,  $P = 0.013$ ; Fig. 3E). Body size did not explain selection for surface  
362 water in equids and ruminants ( $P \geq 0.23$ ; Fig. 3F and 3G).

## 363 **Discussion**

364 We quantified how selection for forage biomass, potential energy intake, and surface water  
365 shaped the movements of free-ranging ungulates across the globe. In support of the FMH,  
366 selection for potential energy intake (i.e., intermediate forage biomass and intermediate forage



367 digestibility) was most frequent among smaller-bodied ungulates. Selecting forage at early to  
368 intermediate states of phenology reflects the higher mass-specific energetic requirements of  
369 smaller-bodied ungulates (Illius & Gordon 1987; Hopcraft *et al.* 2012). In contrast, larger-bodied  
370 ungulates (comprising both equids and larger-bodied ruminants) foraged in a manner distinct  
371 from the central prediction of the FMH. In accordance with our expectations based on hindgut  
372 fermentation, equids selected consistently for proximity to surface water. In contrast to our  
373 expectations based on ruminant digestion coupled with higher absolute energetic requirements,  
374 larger-bodied ruminants did not consistently select for forage biomass. We offer two  
375 explanations for equivocal support of the hypothesis that larger-bodied ruminants should  
376 prioritize high forage biomass: (1) methodological limitations; and (2) taxonomic and functional  
377 diversity.

378         Combined with high-resolution data from GPS-telemetered individuals, remotely-sensed  
379 vegetation indices allow for testing of the FMH across study populations (Wilmers *et al.* 2013).  
380 However, methodological limitations are inherent to such indices, and synthetic studies like ours  
381 should be viewed as complementary to (rather than as a substitute for) intensive, field-based  
382 investigations, in which forage biomass and quality are quantified directly (e.g., Wilmshurst *et*  
383 *al.* 2000, Hebblewhite *et al.* 2008, Geremia *et al.* 2019). This is particularly the case when  
384 remotely sensed vegetation indices—MSAVI and its derivative, IRG—are assumed to be  
385 correlated with forage biomass and potential energy intake. Although we did not validate these  
386 metrics against field-collected data on forage biomass and potential energy intake (i.e., forage  
387 quality), several studies have quantified relationships between forage biomass, forage quality,  
388 and remotely-sensed metrics directly (e.g., Hebblewhite *et al.* 2008, Wilmers *et al.* 2013,  
389 Geremia *et al.* 2019), and found that such metrics are suitable representations of forage biomass

390 and quality. Therefore, we believe that MSAVI and IRG (i.e., remotely-sensed metrics) are  
391 reasonable proxies for forage biomass and potential energy intake, and they are the only way  
392 (with which we are familiar) to conduct standardized tests of the FMH across many study  
393 populations that range across entire landscapes. A major challenge for future research is to  
394 couple field validations of remotely-sensed vegetation indices with the high resolution  
395 movement trajectories afforded by GPS telemetry.

396         Additionally, and at the spatial scale of MODIS, such indices cannot distinguish between  
397 sources of “greenness” resulting from different vegetation types, such as woody plants and  
398 grasses (Archibald & Scholes 2007; Gaughan *et al.* 2013). So, pixel values could be associated  
399 with vegetation that did not necessarily represent forage from an ungulate’s perspective. We  
400 attempted to minimize the effect of this potential limitation by restricting our analysis to defined  
401 growing seasons, and by restricting our analysis to study areas in which dense forest (per Friedl  
402 & Sulla-Menashe 2015) and % tree cover (per Hansen *et al.* 2013) were minimal. Because the  
403 green-up profile in leaves of woody plants is usually constant, the dramatic change in MSAVI  
404 (which we used to define the growing seasons) is mostly associated with the green-up of grasses  
405 rather than green-up of woody plants (Archibald & Scholes 2007; Higgins *et al.* 2011).  
406 Therefore, the potential for such phenological confounding should be restricted to ecosystems in  
407 which woody plants and grasses co-occur in similar proportions yet exhibit different seasonality  
408 (e.g., eastern and southern African savannas and European forests).

409         Differences in the strength and consistency of resource selection were likely due in part  
410 to the relatively high diversity of ruminants in our study, which incorporated 11 genera  
411 exhibiting a >20-fold difference in body size (from 24 kg roe deer to 590 kg African buffalo)  
412 with additional variation in feeding strategies (e.g., unselective grazing, selective browsing,

413 mixed feeding). However, all species of ruminants in our study foraged largely or wholly in the  
414 understory layer or in open rangelands, for which phenological dynamics were captured by our  
415 forage biomass metrics. Our results also are consistent with site-specific studies on ungulate  
416 assemblages, where multiple ruminants coexist via resource specialization, and therefore exhibit  
417 a diverse array of resource selection (Wilmshurst *et al.* 2000; Kartzinel *et al.* 2015).

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

432         Our remotely-sensed imagery of surface water existed at a coarser temporal resolution  
433 compared to our remotely-sensed imagery of vegetation indices, and did not comprise exhaustive  
434 data on all sources of water available to study populations. For example, ephemeral ponds and  
435 streams are not captured by the Global Surface Water Explorer. However, with a resolution of 30

436 x 30 m, the Global Surface Water Explorer constitutes (by far) the most precise data on the  
437 global distribution of surface water (Pekel *et al.* 2016), and we were able to supplement this  
438 remotely-sensed imagery with locally-collected locations of surface water. The strength of  
439 selection for surface water did not depend on availability of surface water within study areas (but  
440 it did depend on variability in the distance to surface water [Fig. S2]) and, per our initial  
441 prediction based on digestive system, the strength of selection for surface water was significantly  
442 stronger for equids than for ruminants. In sum, we believe that such methodological limitations  
443 associated with remotely-sensed imagery of surface water were unlikely to have had undue  
444 influence on our results and associated inferences (but see Text S2). More generally, we believe  
445 that the Global Surface Water Explorer has strong potential as a tool for wildlife and movement  
446 ecologists, and its potential methodological limitations will be overridden by its value in many  
447 study systems.

448 Our study represents a macroecological test of drivers of ungulate resource selection  
449 across the globe. By necessity, our synthetic approach sacrifices some area- and population-  
450 specific precision in attempt to identify general trends (Levin 1992, Brown 1995). For example,  
451 our use of body size as a predictor variable integrates a suite of size-dependent relationships,  
452 including retention time in the digestive tract and cropping rate. In particular, variation in  
453 cropping rates among species has potential to influence resource selection: for a given body size,  
454 a narrower-muzzled species could more efficiently forage on low biomass compared to a wider-  
455 muzzled species (Spalinger and Hobbs 1992). As another example, all ruminant populations in  
456 our study were sympatric with other wild and domestic ruminants, which could influence  
457 resource selection of free-ranging ungulates (e.g., Mishra *et al.* 2004; Kinnaird & O'Brien 2012).  
458 Future efforts to synthesize patterns of resource selection for free-ranging ungulates might

459 incorporate the occurrence and abundance of livestock and population density of the focal  
460 species (through, e.g., the Gridded Livestock of the World mapping project by the United  
461 Nations). Through resource competition, creating barriers to movement (e.g., fences, roads), and  
462 direct interference, humans can suppress the potential for free-ranging ungulates to exploit  
463 spatiotemporal variability in forage biomass, potential energy intake, and access to surface water  
464 (e.g., Sanderson *et al.* 2002; Ogutu *et al.* 2014; Panzacchi *et al.* 2015; Tucker *et al.* 2018; but see  
465 Young *et al.* 2018). By constraining movements of free-ranging ungulates, human activity may  
466 dampen any effects of body size and digestive system on resource selection and result in  
467 deviations from the central prediction of the FMH. Moreover, individual characteristics such as  
468 sex, age, body mass, and reproductive status of individuals strongly affect energy requirements  
469 and thus resource selection by large ungulates (e.g., Forsyth *et al.* 2005; Hamel & Côté 2008;  
470 Saïd *et al.* 2009; Brivio *et al.* 2014). Additionally, physical constraints inherent to different study  
471 areas (e.g., the spatial scale over which variation in forage biomass and potential energy intake  
472 arise) likely influence the movement and resource selection of free-ranging ungulates to some  
473 degree (Aikens *et al.* 2020). Such area- and population-specific variability almost certainly  
474 contributes to differences in resource selection between populations of the same species (e.g.,  
475 khulan populations in western versus southern Mongolia; Text S2), and could explain variation  
476 around the general trends depicted in Figures 2 and 3. Finally, future studies could benefit from  
477 separating different movement states (e.g., foraging, resting, travelling) to explicitly investigate  
478 resource selection during foraging bouts (Fryxell *et al.* 2008; Gurarie *et al.* 2009). Nevertheless,  
479 our analyses point to important generalities—stronger selection of surface water by equids  
480 relative to ruminants, and stronger selection for potential energy intake by smaller-bodied  
481 ruminants—which conform to expectations based on metabolic allometry and digestive system.

482 In combination with intensive, longitudinal field observations within each study population, we  
483 believe that our comparative cross-taxa study has helped illuminate general rules and  
484 contingencies associated with the FMH.

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

495

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### 773 **Figures**

774 Figure 1. Illustrated predictions for resource selection by equids and different sizes of ruminants  
775 during a hypothetical growing season and in a hypothetical landscape. Forage biomass (dark  
776 green line) and potential energy intake (light green line; measured by rate of change in forage  
777 biomass) increase at beginning of the growing season. The potential for maximum energy intake  
778 occurs at the middle of the growing season, when forage biomass is at intermediate levels.

779 Different sizes and shades of grass represent phenological stages of forage biomass and  
780 digestibility. At early phenological stages (i.e., the lightest shade of green grass), potential  
781 energy intake is low because forage biomass is low. At late phenological and senescent stages  
782 (i.e., the darkest shade of green grass and brown grass, respectively), potential energy intake is  
783 low because forage digestibility is low. (A) The Forage Maturation Hypothesis predicts that  
784 ungulates maximize their energy intake by selecting forage of intermediate biomass at  
785 intermediate phenological stages. (B) However, selection for forage characteristics should also  
786 depend on body size. (C) Smaller-bodied ungulates (which exhibit ruminant digestion) should  
787 select most strongly for maximal energy intake (light green), larger-bodied ruminants should  
788 select for forage biomass (dark green), and equids should select for surface water (blue) to meet  
789 their physiological needs.

790 Figure 2. Locations of the study populations (top panel) and mean  $\pm$  SE parameter estimates of  
791 step-selection functions (SSF) for 11 populations of equids (second panel) and 19 populations of  
792 ruminants (third and fourth panels) during growing seasons. Significant variables with 95%  
793 confidence intervals excluding zero are marked by asterisks. Populations are numbered in  
794 increasing order of a focal species' body size: 1-roe deer (n = 23); 2-goitered gazelle (n = 6); 3-  
795 Mongolian gazelle (n = 7); 4-Mongolian gazelle (n = 5); 5-saiga (n = 26); 6-springbok (n = 10);  
796 7-impala (n = 21); 8-mule deer (n = 100); 9-mule deer (n = 78); 10-reindeer (n = 25); 11-red deer  
797 (n = 51); 12-red deer (n = 22); 13-red deer (n = 13); 14-feral burro (n = 10); 15-wildebeest (n =  
798 9); 16-wildebeest (n = 12); 17-wildebeest (n = 13); 18-khulan (n = 7); 19-khulan (n = 9); 20-  
799 onager (n = 9); 21-plains zebra (n = 9); 22-plains zebra (n = 31); 23-Przewalski's horse (n = 14);  
800 24-Przewalski's horse (n = 5); 25-elk (n = 20); 26-elk (n = 7); 27-mountain zebra (n = 5); 28-  
801 Grevy's zebra (n = 7); 29-feral horse (n = 22); and 30-African buffalo (n = 4).

802 Figure 3. Relationship between population-level resource selection coefficients and digestive  
803 system (A, C, E; weighted analysis of covariance [ANCOVA]) and body size (B, D, F, G;  
804 weighted least squares regression). Equid populations more strongly selected surface water after  
805 controlling for the effect of body size (E), but we detected no significant difference in selection  
806 for forage biomass (A) and potential energy intake (C) after controlling for the effect of body  
807 size differences between equids and ruminants. The effect of body size on selection for potential  
808 energy intake was statistically significant for all free-ranging ungulates (D; red dashed line). The  
809 effect of body size on selection for surface water was not statistically significant for equids (F)  
810 nor for ruminants (G).





