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Quantifying water requirements of African ungulates through a combination of functional traits

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Abstract. Climate and land use change modify surface water availability in African savannas. Surface water is a key resource for both wildlife and livestock and its spatial and temporal distribution is important for understanding the composition of large herbivore assemblages in savannas. Yet, the extent to which ungulate species differ in their water requirements remains poorly quantified. Here, we infer the water requirements of 48 African ungulates by combining six different functional traits related to physiological adaptations to reduce water loss, namely minimum dung moisture, relative dung pellet size, relative surface area of the distal colon, urine osmolality, relative medullary thickness, and evaporation rate. In addition, we investigated how these differences in water requirements relate to differences in dietary water intake. We observed strong correlations between traits related to water loss through dung, urine and evaporation, suggesting that ungulates minimize water loss through multiple pathways simultaneously, which suggests that each trait can thus be used independently to predict water requirements. Furthermore, we found that browsers and grazers had similar water requirements, but browsers are expected to be less dependent on surface water because they acquire more water through their diet. We conclude that these key functional traits are a useful way to determine differences in water requirements and an important tool for predicting changes in herbivore community assembly resulting from changes in surface water availability.

Key words: *climate change; dietary water; dung moisture; dung pellet size; evaporation; medullary thickness; physiological traits; surface water dependence; urine osmolality; water loss.*

INTRODUCTION

Variability in temperature and rainfall patterns is increasing, with consequent effects on resource availability for herbivores across Africa. For arid and semiarid regions throughout Africa, a reduction in the amount of precipitation received during the dry season is expected, which will likely trigger more recurrent and severe droughts (Engelbrecht et al. 2015, Bartzke et al. 2018). Droughts will not only influence herbivores indirectly through changes in food availability, but also directly through decreased surface water availability (Gaylard et al. 2003). Most ungulates in drylands and savanna ecosystems require access to surface water to maintain body fluid homeostasis. However, we lack a general

understanding of how ungulate species differ in their water requirements and whether and how changes in surface water availability will affect the community composition of savanna ungulates.

During the dry season, water-dependent herbivores are constrained by their minimum fundamental frequency of drinking (Cain et al. 2012, Chamaillé-Jammes et al. 2013). Dry season distributions of herbivores in relation to surface water (distance to water) are therefore commonly used as a measure of their surface water dependence (Smit et al. 2007, Gereta et al. 2009, Smit 2011, Owen-Smith 2015, Kihwele et al. 2018). However, herbivore distributions are confounded by other factors such as predation risk and food availability, so that distance to water is not a reliable indicator of water dependence. It is now possible to measure drinking frequency from higher resolution GPS data to quantify the degree of surface water dependence (Cain et al. 2012, Curtin et al. 2018), but it is logistically not feasible to collar many individuals and species across broad geographic

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areas. Therefore, we propose to use a combination of functional traits to quantify herbivore water requirements as an alternative approach.

In order to deal with periods of water shortage, ungulates have developed a suite of ecological, physiological, and behavioral adaptations to conserve body water (Cain et al. 2006, Turner et al. 2010, Cadotte et al. 2013). These adaptations allow water loss to be reduced through different channels (Fig. 1) to cope with changes in water availability (Cain et al. 2006). For example, some arid-adapted species exhibit a relatively large surface area to volume ratio of the spiral and distal colon that allows them to reabsorb more water from their dung (Taylor 1968, Maloiy and Hopcraft 1971, Maloiy 1973). Similarly, a relatively thick kidney medulla supports juxtamedullary nephrons with long loops of Henle to concentrate urine and enable arid-adapted species to reduce urinal water loss (Maloiy et al. 1988). However, it is unknown whether different water conservation traits are associated.

Here, we quantified water requirements for 48 African large mammalian herbivore species using six functional traits. We combine data on dung properties collected in Serengeti National Park and Gorongosa National Park with physiological and ecological traits from published studies. We then explore the relationships between minimum dung moisture, dung pellet size, distal colon area, urine osmolality, medullary thickness, and evaporation rate to find the best indicator(s) for water requirements of mammalian herbivores. Subsequently, we investigate the relationships between our predicted water requirements with herbivore feeding types, phylogeny, and classifications of surface water dependence based on literature assessment. Last, we investigated whether

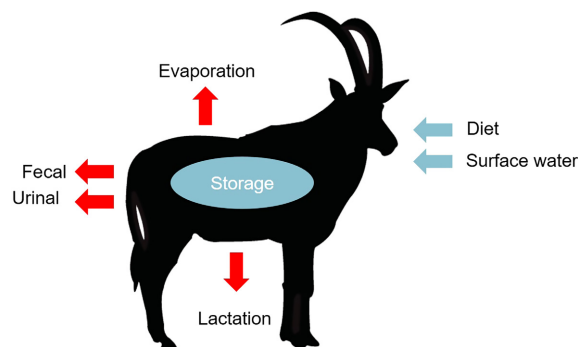


FIG. 1. Overview of the primary components of the water balance of ungulates. Red arrows represent routes of water loss while blue arrows represent water gain (affected by morphology, physiology, and behavior). Some species have specific adaptations to store water (blue circle), such as, for example, fat storage in the camel's hump. Water requirements are lower in species with reduced water loss. Species with higher water requirements are generally more dependent on surface water, but can (partially) decrease this dependence through the intake of water through their diet. Figure adapted from Veldhuis et al. (2019).

species water requirements relate to the amount of water obtained through their diet by comparing our predicted water requirements to dietary water intake using published data on oxygen isotopic enrichment.

METHODS

We quantified water dependence of 48 herbivore species through combining data obtained from previously published studies with data measured in the field. We used six functional traits as indicators of water dependence: minimum dung moisture content, relative dung pellet size, relative distal colon area, urine osmolality, relative medullary thickness, and evaporation rates. We subsequently tested our predictions for a subset of 11 ungulates using experimentally quantified water requirements (percentage weight loss in response to water deprivation). We surveyed the literature for data using the Web of Science, Google Scholar, and cross-referencing to search for each attribute. We extended our data set with data on dung moisture and fresh pellet size in Serengeti National Park and Gorongosa National Park that allowed us to study seasonal variation in dung moisture. Furthermore, we used isotopic oxygen enrichment (see Dietary water intake) as a measure of dietary water intake to investigate which species could decrease their dependence on surface water by using alternative sources of water.

Field data collection

Data were collected in 2018 in both wet (March–May) and dry season (August–October) in Serengeti National Park (SNP), Tanzania, and supplemented with dry season (October) data from Gorongosa National Park (GNP), Mozambique. Samples of 13 herbivore species (impala (*Aepyceros melampus*; $N_{\text{wet}} = 19$, $N_{\text{dry}} = 18$), hartebeest (*Alcelaphus buselaphus*; $N_{\text{wet}} = 3$, $N_{\text{dry}} = 17$), wildebeest (*Connochaetes taurinus*; $N_{\text{wet}} = 5$, $N_{\text{dry}} = 18$), topi (*Damaliscus lunatus*; $N_{\text{wet}} = 18$, $N_{\text{dry}} = 6$), plains zebra (*Equus quagga*; $N_{\text{wet}} = 17$, $N_{\text{dry}} = 18$), Thompson's gazelle (*Eudorcas thomsonii*; $N_{\text{wet}} = 17$, $N_{\text{dry}} = 18$), giraffe (*Giraffa camelopardalis*; $N_{\text{wet}} = 6$, $N_{\text{dry}} = 6$), waterbuck (*Kobus ellipsiprymnus*; $N_{\text{wet}} = 6$, $N_{\text{dry}} = 3$), elephant (*Loxodonta africana*; $N_{\text{wet}} = 6$, $N_{\text{dry}} = 6$), Grant's gazelle (*Nanger granti*; $N_{\text{wet}} = 14$, $N_{\text{dry}} = 4$), common warthog (*Phacochoerus africanus*; $N_{\text{wet}} = 17$, $N_{\text{dry}} = 15$), buffalo (*Syncaerus caffer*; $N_{\text{wet}} = 17$, $N_{\text{dry}} = 13$), and eland (*Tragelaphus oryx*; $N_{\text{wet}} = 18$, $N_{\text{dry}} = 1$)) were collected for dung moisture content and, of these, 11 species for dung pellet size (buffalo did not produce pellets, elephant pellets are highly variable between individuals) in Serengeti National Park. In Gorongosa National Park, we collected data on both dung moisture and pellet size from seven species: sable antelope (*Hippotragus niger*; $N_{\text{dry}} = 13$), oribi (*Ourebia ourebi*; $N_{\text{dry}} = 10$), bush pig

(*Potamochoerus larvatus*; $N_{\text{dry}} = 3$), southern reed-buck (*Redunca arundinum*; $N_{\text{dry}} = 8$), nyala (*Tragelaphus angasii*; $N_{\text{dry}} = 9$), bushbuck (*Tragelaphus scriptus*; $N_{\text{dry}} = 7$), and greater kudu (*Tragelaphus strepsiceros*; $N_{\text{dry}} = 9$). In both parks, drinking water is abundant during the wet season and becomes scarce as the dry season reaches its peak.

Dung pellets were collected between 07:00 and 18:00 and stored in a plastic zipper-closing bag in a cooler box for transport to the laboratory. Pellets were only sampled from observed defecating individuals to be sure that the samples were fresh (collected directly after defecation). In the lab, the length (L), width (W), and height (H) of individual pellets ($N = 3$ for GNP and $N = 9$ for SNP) were measured for each sample using Vernier caliper. Dung moisture content was calculated as the percentage of mass loss between fresh samples (determined back at the lab) and samples dried in an oven until no further mass loss (GNP, 10 d at 60°C) or air-dried (SNP, 14 d).

Dung moisture content

In addition to our dung moisture data from SNP and GNP, we obtained dung moisture data for the dry season and captive animals through our literature search. When multiple sources presented such data, we chose for the minimum value for dry season dung moisture irrespective of its origin. In our final database, dry season dung moisture originated from our own field sampling, Woodall and Skinner (1993), King (1983), De Leeuw et al. (2001), Woodall et al. (1999), Sitters et al. (2014), Clemens and Maloiy (1982), Maloiy et al. (1988), and unpublished data for Grevy's zebra (*Equus grevyi*) from Mpala Research Centre and Conservancy. Dung moisture data of captive individuals with ad libitum water was obtained from Clauss et al. (2004) and Taylor (1968). We then correlated the dung moisture data from the wet season (sufficient water) against the dry season (water limited) collected in Serengeti and the dung moisture of captive individuals (ad libitum) against the dry season dung moisture (water limited) data of our overall database and fitted linear regressions to investigate the plasticity of this trait (Appendix S1: Fig. S1B,C). Dry season dung moisture was lower than wet season moisture for free-ranging individuals and lower than captive individuals, and this difference was larger for species with low dry season dung moisture (slope < 1). We thus used minimum dry season dung moisture in the subsequent analyses as this best represents the species capacity to reabsorb water from dung.

Relative pellet volume

Pellet volume (V) was calculated from the three dimensions ($L \times W \times H$) assuming an ellipsoid shape: $V = 4/3\pi \times 0.5L \times 0.5W \times 0.5H$. Pellet volume did not differ

between seasons (Appendix S1: Fig. S1A) suggesting that pellet volume is a stable trait within species. We thus grouped dung volume estimates from both seasons for further analyses. To correct for species body size, we divided pellet volume by the body mass of each species, because arid-adapted species have smaller pellets than predicted for their body mass (Coe and Carr 1983). Pellet volume is determined by the cross-sectional area of the rectum so that pellet volume is expected to scale allometrically with body mass with an exponent of 0.67. A linear model of the logarithms of pellet volume and body mass for ruminants had a slope of 0.69 (Appendix S1: Fig. S2), which is very close to our assumed relationship of 0.67. Ecosystem and sex-specific body mass data for SNP were obtained from Sachs (1967), except for migrating wildebeest that were taken from Hopcraft et al. (2015). Body mass of bushbuck ($n = 29$) and nyala ($n = 16$) for GNP are unpublished estimates.

Relative distal colon area

Data on the dimensions of the intestines for 15 ruminant ungulates were acquired from Woodall and Skinner (1993). The surface area of the distal colon, where most of the water reabsorption takes place (Woodall and Skinner 1993), divided by the total surface area of both small and large intestine, to correct for body size, was calculated and used as an indicator of the capacity to reabsorb water from dung. This indicator has not previously been used but is analogous to the relative medullary thickness used for the ability to reabsorb water from nephrons. The surface area of the distal colon is the morphological trait that facilitates the resorption of water from dung, similar to the kidney medulla enabling resorption from urine.

Urine osmolality

Urine osmolality data were obtained from Beuchat (1990, 1996), Penzhorn (1988), King (1983), and Cloete and Kok (1986), which all represent maximum urine osmolality values. The maximum was taken when multiple sources presented osmolality measures of the same species as this best represents the maximum capacity of the species to concentrate urine.

Relative medullary thickness

Data on the relative thickness of the medulla (RMT) were taken from Beuchat (1990, 1996) and Cloete and Kok (1986) and calculated from published values on medullary thickness (MT) and kidney volume (KS) (Maluf 1991, 1995, 2002) as $RMT = MT/KS \times 10$, where KS is computed as cube root of the product of the three size dimension, ($L \times W \times H$)^{0.33} (Greenwald 1989, Beuchat 1990). Hippos (*Hippopotamus amphibius*) lack central medulla and thus have little capacity to concentrate urine (Beuchat 1996).

Evaporation

Data on evaporation rates are scarce, as they require controlled experiments in climate rooms. Maloiy (1973) summarizes data from three studies (Taylor 1970, Maloiy and Hopcraft 1971, Maloiy and Taylor 1971) that executed such experiments for 12 ungulate species under two temperature regimes: (1) constant temperature of 22°C and (2) alternating between temperatures of 22°C and 40°C every 12 h, both under conditions with limited water availability (dehydration). Evaporation was higher under the alternating regime for all species, as expected, but the qualitative patterns between evaporation and body mass were similar (Appendix S1: Fig. S3). We used the evaporation rates from the constant temperature regime for our study, because 22°C is quite close to the average dry season temperatures in most of Africa's savannas. Furthermore, this included waterbuck (*Kobus ellipsiprymnus*), which lacked measurements in the alternating treatment because it lost 12% of its body mass within the first 12 h, suggesting it would not survive long under that temperature regime. We corrected for body mass by dividing evaporation rates by body mass^{0.67}, which is the relationship between changes in surface area and volume. Deviations from this general relationship (relative evaporation), were used as a measure of adaption to reduce water loss through evaporation.

Water requirements

The same experiments also yielded unique data on water requirements (Taylor 1968, Maloiy and Hopcraft 1971, Maloiy and Taylor 1971) through gradually reducing drinking water to a point where animals were able just to maintain their weight at about 85% of the initial levels, which was then presented as the minimum water requirements of those species. Also here, we used the water requirement under stable 22°C conditions divided by metabolic weight (body mass^{0.75}) to compare animals differing greatly in size (Taylor 1968). Deviations from this general trend are presented as the relative water requirements.

Predicting water requirements based on the functional traits

We then used the six different traits to predict the water requirements of 48 ungulates for which we had data for at least one of the traits. To obtain a single currency for water requirements, we predicted the dung moisture from the regressions between dung moisture and the other functional traits. We then rescaled these estimates of inferred dung moisture from different traits between 0 and 100 (where 0 represents the minimum observed value and 100 represents the maximum observed value), and then averaged the components of the three different pathways: dung (dung moisture, relative dung volume, relative distal colon areas), urine (urine osmolality, relative medullary thickness), and

evaporation (relative evaporation). An overall ranking is then presented using the mean of the three predictions linked to the three channels.

Dietary water intake

Isotopic oxygen enrichment was used as an indicator of the amount of water obtained through diet relative to drinking surface water (Kohn 1996). $\delta^{18}\text{O}$ values in plant leaves are higher because evaporation enriches the remaining water in the heavy isotope ^{18}O relative to source water (Blumenthal et al. 2017) and $\delta^{18}\text{O}$ values in large herbivores can thus be used as an indicator of the source of water (surface water vs. diet). We used the data set from Blumenthal et al. (2017) where we selected data from sites with a water deficit > 0, which is the annual difference (in mm/yr) between water loss (evaporation and transpiration) and water gain (precipitation). We thus only included areas with low water availability where animals are expected to be water-limited, because this is most informative of the capacity of different species to obtain water from their food. To increase the robustness of our analyses, we only included species with at least three data points in this final data set.

Feeding type

Feeding types were distilled from Owen-Smith (1997), Kingdon and Hoffmann (2013a, b), and Gagnon and Chew (2000), yielding six feeding type categories: obligate grazers (GRO), variable grazers (GRV), variable browsers (BRV), obligate browsers (BRO), frugivores (FRU), and generalists (GEN). Livestock species were not included in the analyses of feeding types.

Water dependence classification

Classification of surface water dependence was taken from Hempson et al. (2015), which aggregated data from Kingdon and Hoffmann (2013a, b) and Wilson and Mittermeier (2011). They classified water dependence into three categories: (1) obtains all water from forage or has physiological adaptations allowing the species to go for long periods without requiring access to surface water (none), (2) requires access to drinking water irregularly but do not display specific physiological adaptations to survive without water for long periods (low), and (3) requires almost daily access to drinking water placing constraints on daily foraging ranges (high).

Data analysis

All statistics were performed in R software version 3.5.1 (R Core Team 2018). ANOVAs, linear regressions and Pearson's correlation (r) were used for all analyses. Pellet volume, body mass, evaporation and urine osmolality were all log-transformed to meet assumptions of normality.

RESULTS

Comparison between different indicators of water loss through dung

All three indicators of water loss through dung were highly correlated (Fig. 2). Dung moisture represents the actual water loss but varies based on water availability (Appendix S1: Fig. S1), while relative pellet size and distal colon area are constant throughout the seasons and provide secondary indices for the capacity to prevent water loss through dung. Herbivore species differed significantly in these physiological and ecological traits related to water loss through dung. Minimum dung moisture content showed strong correlations with relative distal colon area (corrected for total intestine area, Fig. 2A; $r = -0.80$) and with relative pellet volume (corrected for body mass, Fig. 2B; $r = 0.91$). However, the non-ruminant ungulates common warthog (*Phacochoerus africanus*) and plains zebra (*Equus quagga*) did not follow the general trends with relative pellet volume and had relatively larger pellets than the ruminants. We did not have data on distal colon area for non-ruminants so we could not investigate whether they follow the trends we found for the ruminants. No significant differences were found between feeding types for minimum dung moisture content (ANOVA, $F_{6,36} = 2.0$, $P = 0.08$), relative pellet volume (ANOVA, $F_{3,10} = 1.2$, $P = 0.34$), or relative distal colon area (ANOVA, $F_{4,11} = 1.1$, $P = 0.37$).

Relationships between indicators of the different pathway of water loss

We observed strong correlations between indicators of the three different channels of water loss (dung, urine, and evaporation), with the most robust relationship

between dung moisture and urine osmolality. Our results indicate that animals with dry dung have concentrated urine (Fig. 3A; $r = -0.93$), greater relative medullary thickness (corrected for kidney size, Fig. 3B; $r = -0.80$) and low relative evaporation rates (corrected for body mass, Fig. 3C; $r = 0.76$), so that arid-adapted herbivores prevent water loss through all pathways simultaneously. Urine osmolality (ANOVA, $F_{4,15} = 1.8$, $P = 0.18$), relative medullary thickness (ANOVA, $F_{4,10} = 2.9$, $P = 0.08$), and evaporation rates (ANOVA, $F_{3,8} = 0.2$, $P = 0.87$) did not differ between feeding types.

Relating water loss indicators to water requirements

Composite indices of water loss through dung (combining dung moisture, relative pellet size, and distal colon area into a single indicator), urine (combining urine osmolality and relative medullary thickness), and evaporation all predicted the experimentally measured water requirements of large herbivores well (Fig. 4; dung $r = 0.66$; urine $r = 0.83$; evaporation $r = 0.92$). Combining these indices into a single indicator had similar predictive ability to the experimentally measured water requirements (Fig. 4D; $r = 0.83$). Minimum dung moisture was also strongly correlated to water requirements (Appendix S1: Fig. S5; $r = 0.72$).

Predicting water requirements for the African ungulate guild

Our predicted water requirements based on combined indicators of water loss through dung, urine, and evaporation show a wide variety of water requirements among 48 African ungulates, with Kirk's dik-dik (*Madoqua kirkii*) having the smallest and hippo (*Hippopotamus amphibius*) the largest water requirements (Fig. 5). The variation of our prediction

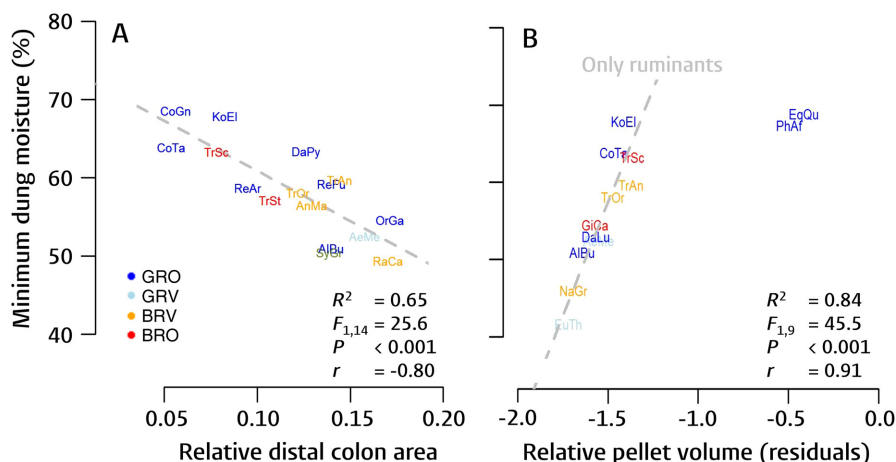


FIG. 2. The relationships between different indicators of water loss through dung. Correlation of minimum dung moisture against (A) relative distal colon area ($y = 73.6 - 128.0x$) and (B) relative dung pellet volume ($y = 145.5 + 58.8x$). Relative pellet volume is expressed as the deviation (residuals) from the expected pellet volume based on body mass (Appendix S1: Fig. S2). Dashed gray lines represent linear regression models that only represent ruminants (excluding EqQu and PhAf in panel B). Colors identify feeding types. Abbreviations represent the first two letters of the genus and species names (see Appendix S1: Table S1).

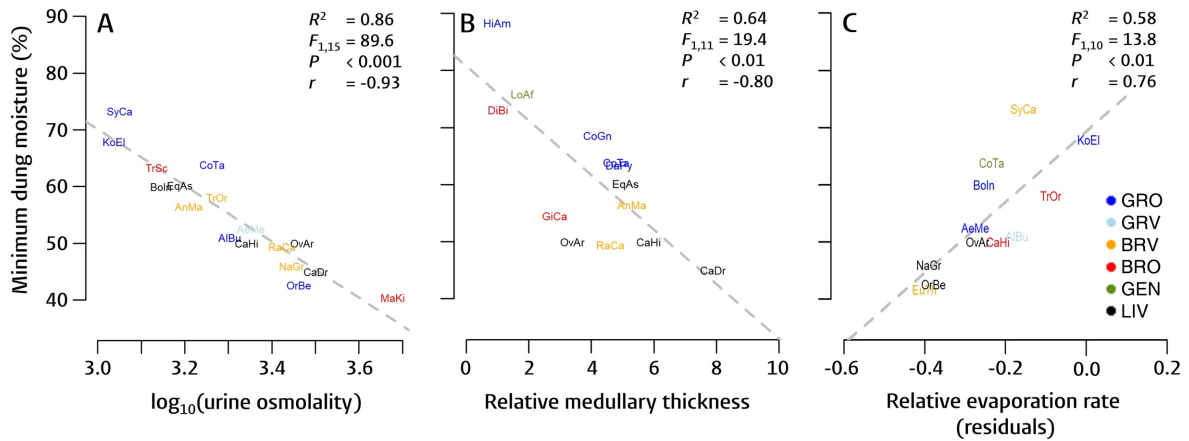


FIG. 3. Relationships between indicators of water loss through dung, urine and evaporation. Correlation of minimum dung moisture against (A) urine osmolality (measured as mOsm/kg H₂O; $y = 218.4 - 49.4 \times \log_{10}(x)$), (B) relative medullary thickness ($y = 80.4 - 35.2 \times \log_{10}(x)$), and (C) relative evaporation rate ($y = 69.3 + 61.8x$). Relative evaporation rate is expressed as the deviation (residuals) from the expected evaporation rate based on body mass (Appendix S1; Fig. S3). Dashed grey lines represent linear regression models. Colors identify feeding type of wild herbivores. Livestock species are presented in black. Abbreviations represent the first two letters of the genus and species names (see Appendix S1; Table S1).

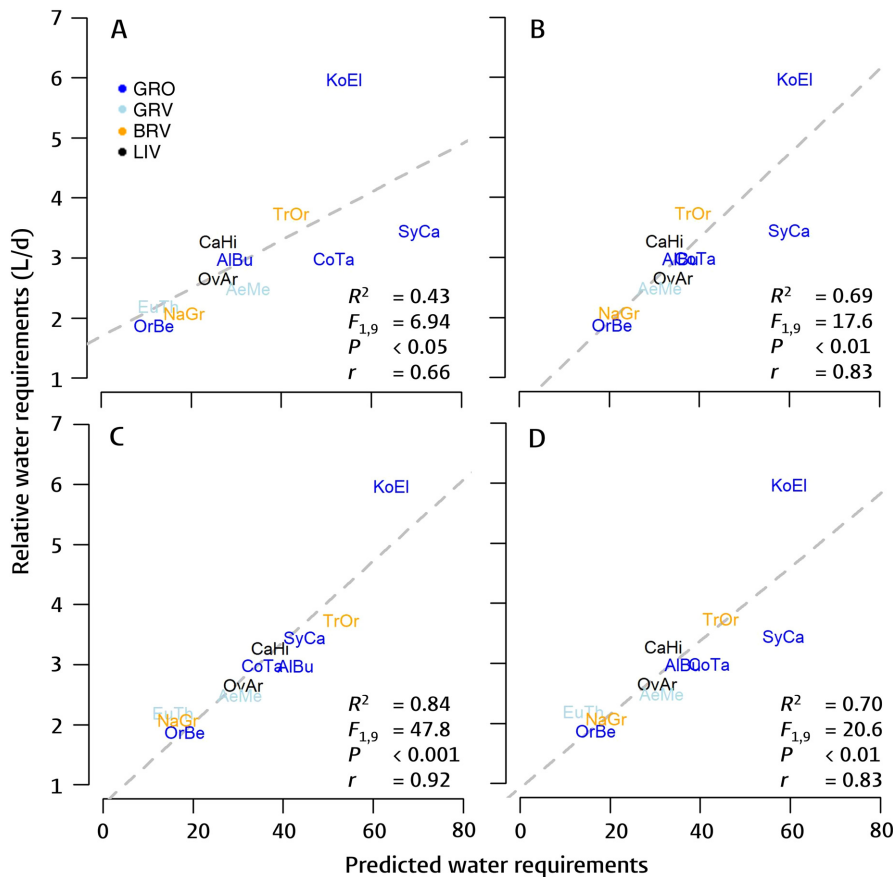


FIG. 4. Relationship between measured water requirements of 11 ungulates and their predicted water requirements based on composite indicators of water loss through (A) dung, (B) urine, (C) evaporation, or (D) a combination of them. Dashed gray lines represent linear regression models. Colors identify feeding type of wild herbivores. Livestock species are presented in black. Abbreviations represent the first two letters of the genus and species names (see Appendix S1; Table S1).

for water requirements is in general agreement with the categories of surface water dependence classifications (ANOVA, $F_{3,44} = 6.9$, $P < 0.001$). Water requirements did not differ between feeding types (ANOVA, $F_{5,42} = 1.5$, $P = 0.20$), even when we excluded non-ruminants (ANOVA, $F_{5,33} = 1.1$, $P = 0.36$). However, we did find a strong phylogenetic signal of water requirements (ANOVA, $F_{15,35} = 7.3$, $P < 0.001$). Non-ruminants, Bovinae (Bovini and Tragelaphini), and Reduncini showed higher water requirements in general,

while the gazelles (Antilopini), horse-like antelopes (Hippotragini), and dwarf antelopes (Neotragini) exhibit low water requirements.

Relationships between dietary water intake and water requirements

Water obtained through food relative to drinking generally decreased with an increase in our predicted water

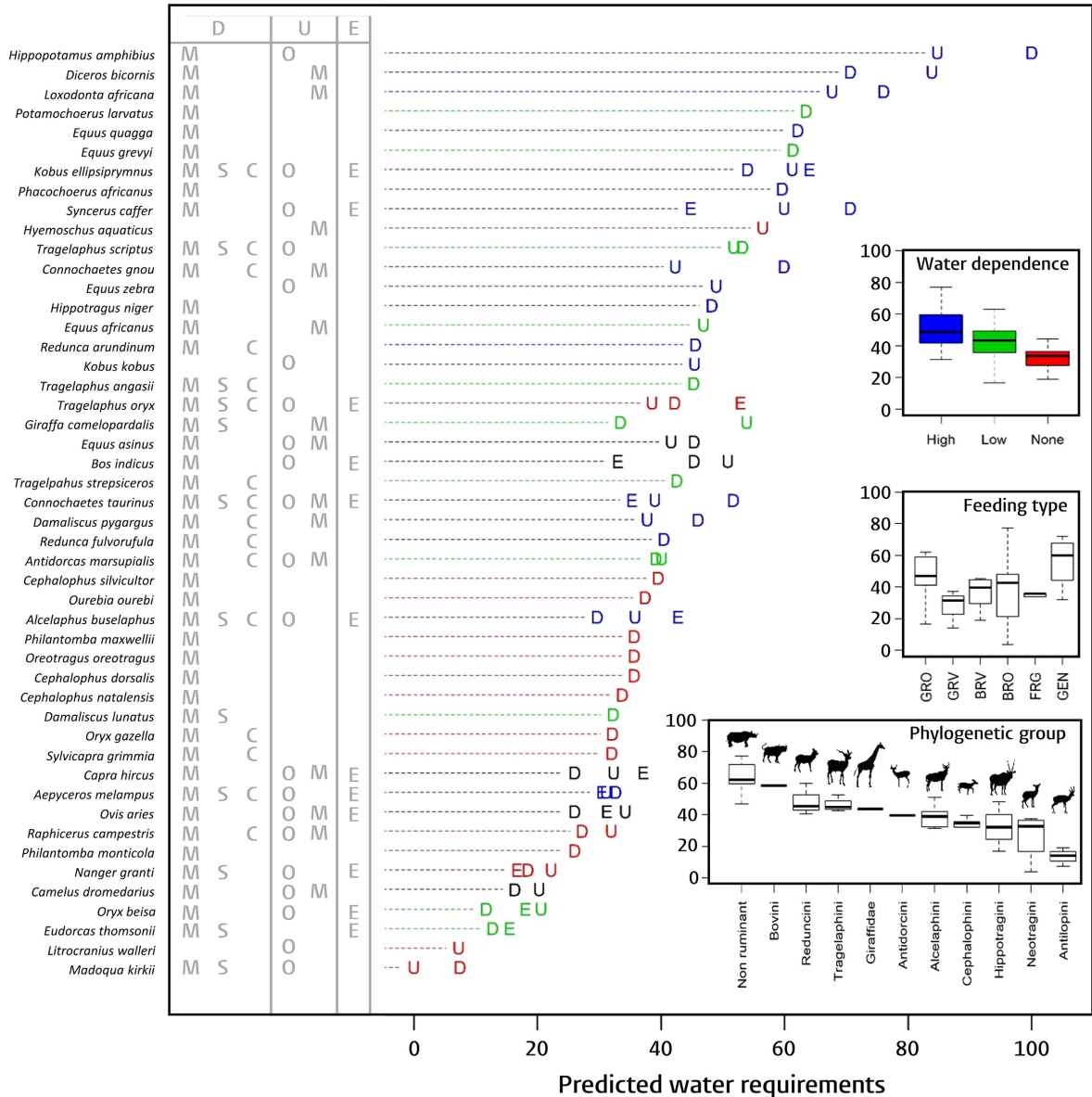


FIG. 5. Predicted water requirements of 48 African ungulates based on composite indicators of water loss through dung (D), urine (U), and evaporation (E). Colors represent water dependence classifications based on literature assessment with three classes: none (red), low (green), or high (blue). Livestock species are presented in black. Insets display the variation of water-dependent classification (top), feeding type (middle), and phylogenetic group (bottom). Box plot components are mid line, median; box edges, 25th and 75th percentile; and whiskers, 1.5 times the interquartile range. Data availability of the six indicators per species are presented in the columns on the left with dung moisture content (M), relative colon area (C) as indicators of water loss through dung (D); urine osmolality (O) and relative medullary thickness (M) as indicators of water loss through urine (U); as well as water loss through evaporation (E).

requirements (Fig. 6; $r = -0.62$), suggesting that species adapted to arid conditions reduce their dependence on surface water by both reducing water loss and increasing dietary water intake. Feeding type did not significantly affect dietary water intake across all ungulates (ANOVA, $F_{4,15} = 1.69$, $P = 0.20$). However, there were significant differences when we limited the analyses to ruminants only (ANOVA, $F_{3,9} = 9.4$, $P < 0.01$). Obligate browsers (BRO) obtained more water from their diet than obligate grazers (GRO; $P < 0.01$), while variable grazers (GRV) and variable browsers (BRV) showed intermediate dietary water intake but marginally insignificant from obligate browsers ($P = 0.06$ and $P = 0.09$, respectively), probably due to their low sample size. Greater kudu (*Tragelaphus strepsiceros*) and Grevy's zebra (*Equus grevyi*) showed significantly higher oxygen isotope enrichment than would be expected based on their predicted water requirements, suggesting that these species can compensate for their relatively high water requirements through dietary water acquisition making them less dependent on surface water than expected.

DISCUSSION

We quantified water requirements for 48 species of African ungulates by combining six functional traits related to water loss. We found these traits to be highly correlated and they accurately predicted the experimentally measured water requirements of a selection of ungulate species, suggesting each single trait is a valuable indicator of ungulate water requirements. African ungulates varied widely in their water requirements and in

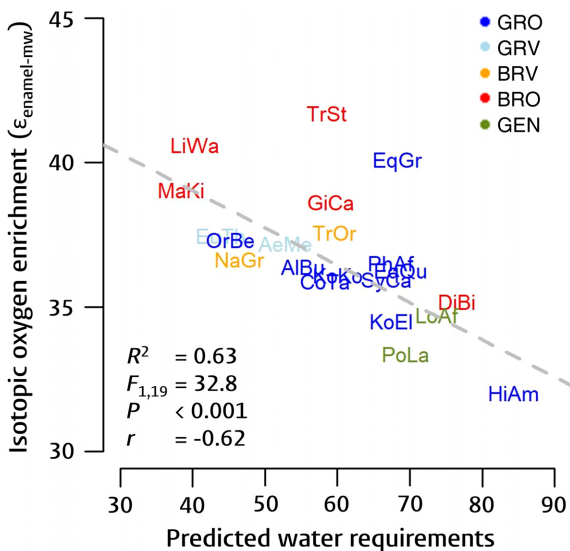


FIG. 6. Amount of water obtained through food relative to drinking as a function of the predicted water requirements of African ungulates. Dashed gray lines represent linear regression models ($y = 44.1 - 0.12x$). Colors identify feeding type of wild herbivores. Abbreviations represent the first two letters of the genus and species names (see Appendix S1: Table S1).

general, water-independent species obtain more water through their food relative to drinking, thereby reducing their dependence on surface water. In general, our predicted water requirements were in line with classifications based on literature assessments. Altogether, our results show great potential for using functional traits to predict ungulate water requirements, specifically for large herbivore species assemblages.

The strong correlations between minimum dung moisture and all other indicators of water loss provide evidence that herbivore species reduce water loss through multiple pathways simultaneously, such that species producing dry dung also produce highly concentrated urine (Maloiy 1973). However, some of these traits are more plastic than others. Dung moisture was higher in the wet season than dry season and a higher moisture content was observed in captive individuals provided with free access to drinking water than free-ranging individuals, which is in agreement with previous work (Maloiy 1973, Edwards 1991, Rymer et al. 2016). Not surprisingly, urine osmolality also varies with water availability and evaporation varies with both water availability and ambient temperature (Taylor 1968, Maloiy 1973). The flexibility of these traits appears to be an important physiological and ecological adaptation to (seasonal) changes in water availability (Woodall and Skinner 1993) and thus provide a more sensitive and plastic variable to assess water requirements in temporally and spatially heterogeneous landscapes. Dung moisture measurements obtained through water deprivation experiments are thus a better indicator of their water requirements, as the dung moisture of wild ungulates is affected by the local availability of water. In contrast, anatomical adaptations such as the dimensions of the kidney and intestine, and consequently dung size, are likely to be more constant and may thus provide a better indication of the capacity to conserve water. We therefore suggest that dung moisture is an easy-to-measure (flexible) index of the hydration state of African ungulate species, while relative dung size is an easy-to-measure (static) index of the species' capacity to conserve water.

It is important to stress that our findings mostly addressed between-species comparisons and it is unclear whether these patterns hold between individuals within species. Not all species showed plasticity in dung moisture content between seasons (Fig. 1B). For example, dung moisture of buffalo and elephant was around 80% in both seasons. Investigations of the generality of these patterns within individuals, between individuals of the same species and between species and how this relates to evolutionary history and developmental plasticity remains to be investigated.

Our interpretation of the data must be tempered by some limitations. First, we do not have a complete list of traits measured for all species under the same environmental conditions. Our predicted water requirements for some species are based on a single trait measure, which make those predictions less reliable.

Second, our data are biased toward ruminant herbivores. Although non-ruminants followed the general patterns for the correlations between minimum dung moisture, urine osmolality, and relative medullary thickness, we do not have data on intestine dimensions or evaporation rates for these species. Furthermore, plains zebra and warthog (non-ruminants) were strong outliers to the general trend between minimum dung moisture and relative dung pellet volume (Fig. 2B). Zebra and warthog have relatively large dung pellets that provide a small surface area for water resorption through the colon (Woodall et al. 1999). Our data suggest that, in general, non-ruminants are more water dependent and thus more vulnerable to loss of surface water. Nevertheless, non-ruminant species like Grevy zebra and desert warthog (*Phacochoerus aethiopicus*) inhabit very dry areas and thus challenge this observation. Future work should thus aim to augment the trait data set, specifically for non-ruminants, to improve the accuracy of the predictions and the robustness of our conclusions about the generality of the observed patterns.

Third, the isotopic oxygen enrichment that we used in our analysis is a valuable tool but has important limitations. For example, fruits do not exhibit oxygen enrichment (Kohn 1996), thereby reducing the reliability of the method for species with a high percentage of succulent fruit in their diet. This calls for further research to investigate the proportional contribution of each food component on the overall water budget of the species. Despite these limitations, our study shows great potential for using functional traits to predict ungulate water requirements.

While our predicted water requirements generally were in line with classifications based on literature assessments, there were some intriguing inconsistencies between the two. We predicted relatively lower water requirements for some species (beisa oryx, Thompson's gazelle, impala, and hartebeest) and higher water requirements for others (eland, Grevy zebra, bushpig, and bushbuck). Deviations toward lower predicted water requirement could result from species using habitats closer to water for reasons other than water requirements that led observers to believe the species was water dependent. For example, impala are generally found close to water and are therefore often classified as water dependent even though their water requirements have been shown to be low (Maloiy 1973). Water dependence classifications of hartebeest are ambiguous; some authors place them in the water-bound group (Western 1975) whereas others classify them as water independent (Woodall and Skinner 1993). Our prediction is based on functional traits and thus is less confounded by ecological factors such as food availability or predation risk.

Our deviating predictions toward higher water requirements likely result from the difference between water requirements and surface water dependence. Species with higher water requirements can reduce their

dependence on surface water through increased intake of preformed water. For example, eland are generally classified as water-independent (Western 1975, Woodall and Skinner 1993), even though experiments have shown they have about the same water requirements as buffalo (Taylor 1968). Eland could increase independence of surface water by means other than water conservation such as the selection of succulent food (Taylor 1969). Increased intake of preformed water could thus decrease surface water dependence regardless of their basic water requirements and might be of particular importance for species that are closely related to more water-dependent lineages (Bovinae, Equidae, Suidae).

In general, there was a negative correlation between isotopic oxygen enrichment and water requirements, with those species relying on preformed water in their diet scoring lower on our predicted water requirements based on functional traits. Overall, species with lower water requirements are thus also less dependent on acquiring water through drinking. Nevertheless, specific species such as greater kudu and Grevy's zebra, recognized for occupying drier areas, are predicted to have relatively high water requirements but reduce surface water dependence through behavioral adaptation such as increased dietary water intake and thus can decrease surface water dependence if sufficiently high moisture forage is available. Also, ruminant browsers showed significantly higher dietary water intake than ruminant grazers, even though feeding type did not affect their water requirements, suggesting that browsers are less dependent on acquiring water through drinking than grazers. The leaf water content of grasses that die off aboveground during the dry season is generally lower than that of woody plants that remain green. The resulting higher dietary water intake is expected to make browsers less surface water-dependent than grazers (Western 1975, Kay 1997), even though their water requirements are similar. Altogether, our results suggest that the reduction of surface water dependence through increased intake of preformed water can be very important, is difficult to quantify and very species specific. Detailed investigations of the proportional contribution of each food component to the overall water budget of each species are required.

CONCLUSIONS

The expected changes in climate and land use, compounded by an increase in the frequency and intensity of drought, will further exacerbate the limited water supply in savanna ecosystems, especially during the late dry season. As such, the quantification of herbivore water requirements is vital to guide management and conservation of herbivores. Managers can measure the dry season dung moisture and compare those with our predictions to evaluate relative water deficiency between species. They can use our predictions to evaluate the suitability of the area for potential reintroductions given

the surface water availability in the area. Also, when conservation of water-independent species, which can be identified based on our predictions, is high priority, managers should consider decreasing surface water availability throughout the area. We conclude that functional traits are a great tool to predict ungulate water requirements. Each of these traits provide specific information about ungulate water balance and their combination provides a convenient estimate of water requirements. This quantification provides opportunities to explore the relationship between herbivore water requirements and other important constraints for large herbivores, such as predation, thermoregulation and foraging. Expanding this approach to a more complete data set and a greater range of species will further elucidate the role of water requirements in structuring African ungulate communities.

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SUPPORTING INFORMATION

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DATA AVAILABILITY

Data are available in the Dryad Digital Repository at <https://doi.org/10.5061/dryad.2jm63xsk0>.