Water economics of African savanna herbivores: how much does plant moisture matter?

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Author's Contributions

Jeremy A. Van Driessche and Ryan A. Long conceived the ideas and designed the study;
Jeremy A. Van Driessche, Simon Chamaillé-Jammes, Robert M. Pringle, and Ryan A. Long developed methodologies;
Jeremy A. Van Driessche, Ciara M. Nutter, Arjun B. Potter, Robert M. Pringle, and Ryan A. Long collected and analyzed the data;
Jeremy A. Van Driessche and Ryan A. Long wrote the manuscript;
All authors contributed critically to the drafts and gave final approval for publication.

Conflicts of Interest

The authors declare no conflicts of interest.

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ABSTRACT

1. Water is an essential and often limiting resource that pervades all aspects of animal ecology. Yet, water economics are grossly understudied relative to foraging and predation, leaving ecologists ill-equipped to predict how the intensifying disruption of hydrological regimes worldwide will impact communities. For savanna herbivores, reliance on surface water can increase exposure to predators and competitors, and thus strategies that reduce the need to drink are advantageous. Yet, the extent to which increasing dietary water intake while decreasing water loss enables animals to forego drinking remains unknown.
2. We studied water budgets of sympatric African savanna antelopes that differ in size, bushbuck (*Tragelaphus sylvaticus*, ~35 kg) and kudu (*T. strepsiceros*, ~140 kg). We hypothesized that both species compensate for seasonally declining water availability by increasing consumption of moisture-rich plants and reducing fecal water loss, and that these adjustments are sufficient for small-bodied—but not large-bodied—herbivores to avoid spending more time near permanent water sources as the dry season advances. We tested our predictions using temporally explicit data on antelope movements, diets, plant traits, and drinking behavior in Gorongosa National Park, Mozambique.
3. Water content declined between the early and late dry seasons in roughly half of plant taxa consumed by antelope. Although both species reduced fecal water loss and shifted their diets towards relatively moisture-rich plants as the dry season progressed, dietary water intake still declined. Contrary to expectation, kudu reduced selection for surface water in the late dry season without adjusting total time spent drinking, whereas bushbuck increased selection for surface water.

4. We developed a generalizable approach for parsing the importance of dietary and surface water for large herbivores. Our results underscore that variation in surface-water dependence is a key organizing force in herbivore communities but also show that simple allometric predictions about the behavioral and ecological consequences of this variation are unreliable. Understanding wildlife water economics is a research frontier that will be essential for predicting changes in species distribution and community composition as temperatures rise and droughts intensify.

KEYWORDS

African savannas; animal movement; animal-borne sensor (biologger); body mass; dehydration; dietary water content; DNA metabarcoding; Gorongosa National Park, Mozambique

INTRODUCTION

Water distribution and accessibility govern ecological patterns and processes across levels of organization, from the behavior and physiology of individual organisms (Cain et al., 2006) to species distributions and community composition (Gaylard et al., 2003). Globally, water availability drives spatiotemporal variation in biodiversity and is the best predictor of species richness across the tropics and subtropics (Hawkins et al., 2003). Many of these ecosystems, such as tropical savannas, exhibit marked seasonal variation in rainfall, temperature, and primary productivity (Chamaillé-Jammes & Fritz, 2009; Chamaillé-Jammes et al., 2007). In such environments, we should expect animals to exhibit physiological and behavioral strategies for enduring periods of scarcity and resource competition.

Large herbivores are ecologically pivotal (Pringle et al., 2023) and have been undergoing size-biased extinction since the late Quaternary owing to human pressure and climate change (Barnosky et al., 2004; Faith et al., 2018; Smith et al., 2018). Given current and projected intensification of warming, drought, and ecohydrological disruption, understanding how savanna herbivores maintain water balance is essential for managing populations and ecosystems (Veldhuis et al., 2019). Especially during dry periods, savanna herbivores may confront tradeoffs between access to surface water and feeding opportunities or predation risk (Redfern et al., 2003). In the face of these tradeoffs, mechanisms that reduce surface-water dependence (i.e., the amount of time an animal must spend drinking to meet its water intake requirements) should confer a fitness advantage by allowing individuals to range farther across the landscape, by reducing spatial overlap and competition with more water-dependent species, and by limiting vulnerability to ambush predators that concentrate their activity around water sources (Mosser et al., 2009; Valeix et al., 2009).

Interspecific variation in water requirements depends on multiple morphological and physiological traits, some of which are essentially fixed and cannot be dynamically tuned in response to ecological conditions. Body size is one such factor: all else equal, larger species tend to require more water, although this relationship is noisy in ungulates owing to variation in other traits associated with water use and conservation (Kihwele et al., 2020; Taylor, 1968a, b; Veldhuis et al., 2019). Within such hardwired constraints, however, individuals might reduce their need to drink by adjusting their physiology or behavior. For example, ungulates in dry conditions commonly increase water resorption in the distal colon to reduce fecal water loss (Cain et al., 2006; Ghobrial & Cloudsley-Thompson, 1966; Maloiy & Hopcraft, 1971). Individuals might also be able to reduce dependence on drinking by obtaining more water from food (preformed water). Preformed water can be a significant component of ungulate water budgets (Taylor, 1968a, b) and is thought to explain, for example, why browsers (with comparatively moisture-rich diets of forbs and trees) tend to be less surface-water dependent and more drought resistant than grazers (Abraham et al., 2019; Hempson et al., 2015; Kay, 1997; Veldhuis et al., 2019).

Few studies have attempted to empirically partition preformed and surface water fractions of ungulate water budgets, and those focus mainly on species-level differences (Taylor, 1968a, b; Veldhuis et al., 2019). We are not aware of any study that has tested the extent to which individuals of different species dynamically adjust dietary water intake in response to environmental pressures, and whether this relaxes their reliance on surface water. Indeed, despite outstanding early experimental work (Taylor, 1968a, b; Taylor, 1970a, b; Taylor et al., 1974), our understanding of ungulate water budgets remains limited. This is in part because it is difficult to measure water intake directly in free-ranging animals, suggesting a need for pragmatic estimation procedures.

We sought to understand seasonal variation in preformed-water ingestion and its implications for surface-water dependence in a mesic African savanna with a long dry season. We focused on two common, sympatric species of browsing antelopes that are closely related and ecologically similar but differ fourfold in body size: Cape bushbuck (*Tragelaphus sylvaticus,* ~35 kg) and greater kudu (*T. strepsiceros,* ~140 kg). We hypothesized that as plants senesce and surface water becomes scarce late in the dry season, antelopes try to compensate for declining dietary water intake by shifting their diets towards plants with higher water content and reducing fecal water loss. We also hypothesized, however, that the consequences of these adjustments would differ between species. Bushbuck are smaller and apparently less capable of reducing fecal water loss than kudu (Veldhuis et al., 2019; Woodall & Skinner, 1993), perhaps because a shorter, narrower large intestine translates to reduced surface area available for water resorption in the distal colon. However, their smaller size also comes with a correspondingly greater surface-area-to-volume ratio and thinner boundary layer (Porter & Gates, 1969; Speakman & Król, 2010), which increases rates of heat exchange and, in theory, reduces water requirements for thermoregulation via evaporative heat loss. We therefore predicted that even if bushbuck are not capable of removing water from their feces to the same extent as kudu, diet switching and fecal water conservation would still be sufficient for bushbuck to avoid moving closer to permanent surface water as the dry season progressed. In contrast, we predicted that kudu would be forced to increase proximity to surface water and time spent drinking during the dry season owing to their larger size and correspondingly lower surface-area-to-volume ratio and thicker boundary layer. We used selection for surface water (i.e., use of surface water sources relative to their availability; quantified for both species) and amount of time spent drinking (for kudu only) as proxies for surface-water dependence.

MATERIALS AND METHODS

Study area.– Mozambique’s Gorongosa National Park (18.96°S, 34.36°E) is characterized by substantial spatiotemporal variation in water availability and distribution (Tinley, 1977). Our 10-year study of spiral horned antelopes (*Tragelaphus* spp.) in Gorongosa focuses on the core of the park, including Lake Urema and surrounding floodplain grasslands, as well as *Acacia*, palm, and broadleaf savanna woodland habitats (Fig. 1) (Atkins et al., 2019; Daskin et al., 2023; Pansu et al., 2019; Stalmans et al., 2019; Walker et al., 2023b). From 2012–2022, median rainfall in this area was 1037 mm (interquartile range 722–1420 mm), >90% of which fell during the wet season (November to April). Conversely, <20 mm of rain typically falls each month during the dry season (May–October), reducing availability of surface water. Rainfall during this study was in the 50th – 75th percentile range (1013 mm in 2021, 1452 mm in 2022).

***Study species*.–**Cape bushbuck and greater kudu diverged roughly 5 Mya and are sympatric in savannas across much of eastern and southern Africa. They have similar life histories, habitat preferences, and diets; both are strict browsers (Daskin et al., 2023). These traits enabled us to focus, with limited noise arising from phylogenetic distance, on how the difference in body size between the two species influenced the behavioral and physiological strategies they used to cope with changes in water availability during the dry season.

***Animal capture and handling*.–** In July 2021 and June 2022, we captured adult bushbuck (*n* = 13, 10F:3M, in 2021; *n* = 13, 9F:4M, in 2022; mean body mass = 33.6 kg, range = 23.3–56.7 kg) and kudu (*n* = 13, 11F:2M, in 2021; *n* = 10 F in 2022; mean body mass = 123.7 kg, range = 101.9–159.7 kg) as part of the ASHAMED project (Allometry of Spiral-Horned Antelopes: Movement Ecology & Diet, 2014–present), a long-term study of spiral-horned antelope ecology in Gorongosa (Daskin et al., 2023; Walker et al., 2023b). We chemically immobilized individuals via remote injection of a combination of thiafentanil (bushbuck: female = 2.5 mg, male = 3 mg; kudu: female = 8 mg, male = 10 mg), ketamine (bushbuck: female = 60 mg, male = 60 mg; kudu: female = 100 mg, male = 100 mg), and azaperone (bushbuck: female = 15 mg, male = 20 mg; kudu: female = 20 mg, male = 10 mg). We fit each individual with an iridium satellite GPS collar (VERTEX Lite, Vectronic Aerospace) programmed to record locations every 3–30 min for kudu (a temporary switch to 3-min fixes was implemented as part of a related study of fine-scale movements by kudu) and every 60 min for bushbuck. Collars were remotely triggered to drop off 1 year after deployment. All animal-handling procedures were approved by the Institutional Animal Care and Use Committees of the University of Idaho (Protocol No. IACUC-2019-32) and Princeton University (Protocol No. 2075F-16) and were in accordance with guidelines established by the American Society of Mammologists (Sikes & The Animal Care and Use Committee of the American Society of Mammologists, 2016). Research was conducted under permits granted by the Department of Scientific Services at Gorongosa National Park (Permit Nos. PNG-DSCi-C190-2021 and PNG-DSCi-C223-2022).

***Diet composition*.**–We quantified composition of bushbuck and kudu diets via fecal DNA metabarcoding, following protocols used in Gorongosa since 2013 (Atkins et al., 2019; Branco et al., 2019; Daskin et al., 2023; Guyton et al., 2020; Pansu et al., 2019, 2022; Potter et al., 2022; Walker et al., 2023a, b). During immobilizations, we collected a fecal sample from the rectum of each individual. To evaluate changes in diet over the course of the dry season, we collected additional fresh fecal samples from collared individuals of both species in the early (May/June 2022; *n* = 18 bushbuck, 28 kudu), middle (July/August 2021; *n* = 25 bushbuck, 32 kudu), and late (September/October 2021; *n* = 15 bushbuck, 16 kudu) dry season (total *n* = 188). These additional samples were collected as in Walker et al. (2023a): we used GPS data and radiotelemetry to relocate collared individuals and then observed them through binoculars from distances of 10–100 m. When an animal defecated, we noted its distance from the observer and the nearest landmarks and then searched the area and collected >5 fecal pellets in a plastic bag, which we stored on ice until we returned to Gorongosa’s laboratory. We homogenized each sample in the collection bag and transferred a subsample into a labeled tube containing silica beads and preservation buffer (Xpedition Stabilization/Lysis Solution, Zymo Research Corporation). We vortexed tubes for 1 min to lyse cells and then froze them at -80°C. Before transport to the U.S., each sample received an antiviral heat treatment (72°C for 30 min) and was refrozen as dictated by the U.S. Department of Agriculture (Permit 130123 to R.M.P.).

Following established protocols, we amplified the P6 loop of the chloroplast *trn*L(UAA) intron using primers with unique 8-nt tags at the 5' end, which enabled us to pool uniquely identifiable PCR products for sequencing in a single high-throughput run (Taberlet et al., 2007). Extractions were conducted in small batches with positive and negative controls; PCRs were conducted in triplicate to monitor reproducibility; and low-quality outlying PCR replicates were discarded (Pansu et al. 2022). Libraries for each year (2021, comprising mid- and late-dry season, and 2022, comprising the early dry season) were sequenced separately on a MiSeq v3 600nt and processed using OBITools (Boyer et al., 2016). We discarded low-quality sequences, and the remainder were considered operational taxonomic units (mOTUs). After rarefying to the minimum number of sequence reads per sample (990 for 2021; 2,000 in 2022) and excluding mOTUs accounting for <1% of reads per sample, the dataset included 187 unique plant taxa (136 mOTUs each in 2021 and 2022). We identified mOTUs by matching them to a local reference library of DNA sequences from plants collected in Gorongosa (Pansu et al., 2019); mOTUs that matched this database with <98% identity were identified using a global reference library derived from the European Molecular Biology Laboratory database (September 2022 release). We calculated the relative read abundance (RRA) per sample by dividing the rarefied read count of each mOTU by cumulative rarefied read depth (Deagle et al., 2019).

We used permutational multivariate analysis of variance (perMANOVA) to test for seasonal differences in dietary dissimilarity between species and visualized results using nonmetric multidimensional scaling (NMDS; Daskin et al., 2023; Walker et al., 2023a, b).

Dietary and fecal water content.–We used metabarcoding results and plant relative abundance to generate a list of 32 focal plant species, including those most commonly eaten by bushbuck and/or kudu during the dry season. We collected green leaves and stems (petioles) from 3 individuals of each plant species in July (mid dry) and October (late dry) 2021 and May (early dry) 2022 to quantify changes in preformed water content of those species during the dry season (minimum leaf wet mass = 1 g) (Table A.1, Fig. A.1). Total rainfall during May was nearly equivalent during 2021 (19 mm) and 2022 (16.5 mm). We worked with a local botanist to locate at least three representative individuals of each plant species in the habitat in which it was most commonly found (most species occurred either predominantly or exclusively in a single habitat, e.g., floodplain or savanna woodland). We recorded the locations of those individuals and returned to the same general area (i.e., within 200 m) to collect samples in each of the three seasons (early, mid, and late dry). All samples were obtained ≥100 m from a surface water source. Samples were weighed immediately after collection using a Pesola Balance Light Line spring scale (10-g scale with 0.1-g precision for samples <10 g; 100-g scale with 1-g precision for samples >10 g), dried to a constant mass at 100°C, and then reweighed to calculate water content as a proportion of wet mass. We calculated preformed water content using the following equation, where *W* is the weight of plant material:

$$Preformed\ Water\ (\%) = \frac{W_{wet} - W_{dry}}{W_{wet}}\ x\ 100$$

We combined data on diet composition with estimates of plant water content to calculate weighted averages of preformed water in each antelope diet using the RRA of each plant species in the diet as the weighting factor (Potter et al. 2022). We then estimated mean preformed water content in the diets of bushbuck and kudu during the early, mid, and late-dry seasons as the weighted average of preformed water content across individuals using the total proportion of the diet accounted for as the weighting factor (i.e., individuals whose diets we knew with greater certainty had more influence on the estimated species-level mean, cf. Atkins et al., 2019; Becker et al., 2021; Branco et al., 2019; Daskin et al., 2023; Potter et al., 2022; Walker et al., 2023a); the mean RRA of mOTUs for which we had data on water content was 69% (range 50–92%) for bushbuck and 81% (range 53–100%) for kudu. To probe the repeatability of any trends observed in data from our study, we conducted the same analysis using fecal samples collected by the ASHAMED project from 2014–2022 with RRA ≥ 80% ($n_{bushbuck}$ = 145, n_{kudu} = 124; mean RRA for bushbuck and kudu = 89% and 93%, respectively).

Throughout the study, we set aside a subset of fecal samples collected for diet analysis to estimate fecal water content (*n* = 62 bushbuck, 65 kudu). Samples were weighed using the same spring scale and dried to a constant weight at 100°C. We calculated the water content of fecal samples (%) using the same equation used to calculate water content of plants (Lee et al., 2009).

***Selection for surface water*.**–We quantified selection for surface water at the home-range scale (3rd-order selection *sensu* Johnson, 1980) during the 2021 dry season (5 July–31 October 2021) using resource selection functions (RSFs) and a use-availability design (Boyce et al., 2002; Johnson et al., 2006). We used 100% minimum convex polygons (MCP) estimated from each individual's GPS locations (*n* =12 bushbuck, 12 kudu) to delineate home-range boundaries (for defining available habitat). We generated a set of random points equal to the number of used points within each home range per week of the dry season (*n* = 17 weeks, weekly mean number of used points: bushbuck = 166; kudu = 1,011) to assess temporal changes in selection for surface water. We used high-resolution photographic imagery (10-cm accuracy) and a digital terrain model (DTM) of Gorongosa derived from airborne light detection and ranging (LiDAR) data collected in August 2019 (mid-dry season; details in Daskin et al., 2023, Walker et al., 2023a) to hand-digitize rivers within our study area. Perennial ponds (pans) were digitized from satellite imagery (Stalmans, 2019). We used the *near* function in ArcGIS 10.8.1 to calculate the distance between each used or random location and the nearest surface water source, whether river or perennial pan. We standardized all distances by subtracting the mean and dividing by the standard deviation (Cade, 2015; Kutner et al., 2004). We then fit generalized linear mixed-effects models (Bolker et al., 2009; Gillies et al., 2006; Zuur et al., 2009) with a binomial error distribution and logit link function to the used (antelope GPS locations, coded 1) and random (available locations within each home range, coded 0) locations in *lme4* (Bates et al., 2022). We fit separate models for each species on both seasonal (i.e., all dry-season data included) and weekly (i.e., separate models fit for each week) bases. All models included random intercepts and slopes (Zuur et al., 2009) grouped by individual animal, such that the effect of distance to surface water (the sole predictor variable) on selection was allowed to vary among individuals.

We used simple linear regression to quantify changes in the strength of selection for surface water (quantified using standardized coefficients from weekly RSFs) across the dry season. We fit weighted versions of these models, using the inverse of the standard error associated with each GLMM coefficient as the weighting factor to account for uncertainty in estimated coefficients. Finally, we used a two-sample *t*-test to compare mean distance to water (a commonly used proxy of surface-water dependence) between bushbuck and kudu, independent of the RSFs.

***Surface water consumption by kudu*.–** In 2021, we affixed 80-g biologgers capable of recording up to 900 h of 8-kHz audio data (Miquel et al., 2022) to each of 8 female kudu collars (Fig. A.2) to record continuous sound data. We could not attach audio loggers to bushbuck collars owing to their much smaller circumference. We used audio-logger data in conjunction with GPS-collar data to identify drinking bouts and quantify their duration. Miquel et al. (2022) provide a detailed description of the components and construction of the audio loggers. Audio loggers recorded continuously until the batteries failed 6–51 days after deployment ($\bar{x}$ = 33.7 days; 1 logger did not record any usable data). We collected loggers when GPS collars dropped off the following year. We used kudu movement data (3-minute fixes for the first 3-4 weeks, followed by 30 min fixes), in combination with LiDAR imagery, to inform when to review audio-logger data to identify drinking bouts (i.e., based on proximity of collared kudu to a water source; Fig. A.3). We reviewed audio data both aurally and visually via analysis of spectrograms in Audacity 3.2.5 (Audacity Team 2023; Fig. A.3) for approximately 15 min before and after GPS data indicated an individual was near a water source to minimize the possibility of missing drinking bouts. We identified drinking bouts based on the sound of disturbed water and regular, rhythmic swallowing, in combination with the spectrogram (Wijers et al., 2018, 2021). Drinking-bout duration was considered additive if the same individual drank multiple times during the same visit to a water source. In total we recorded 102 drinking bouts by kudu.

To validate the audio recordings as an effective means of identifying drinking bouts by kudu, we used GPS locations from collared individuals in 2021 to estimate the number of visits to perennial pans and the corresponding number of drinking bouts (not all visits to pans lead to drinking). We started by calculating the mean radius of 2,486 pans that were digitized as polygons in a subset of our study area ($\bar{x}$ = 20 m). In the larger point-based pan layer that fully covered the extent of our study area (*n* = 5,074 pans, Stalmans 2019), each point represented the center of a perennial pan. We therefore buffered that layer using a radius of 33 m—20 m average pan radius + 13 m GPS collar error—and used GPS locations obtained during our 7-week focal period to determine when each collared individual was likely near a pan. GPS locations that fell within 33 m of the center of a pan were sorted temporally to distinguish and enumerate separate pan visits for each collared individual. We estimated the number of drinking bouts for each kudu by scaling the number of pan visits by the proportion of visits that led to drinking bouts, which we estimated from camera trap videos (Bushnell Trophy Cam E3, *n* = 38 cameras placed at perennial pans from August–October, 2021): of 9 video recordings of female kudu at perennial pans, 6 included drinking behavior (67%). We compared the weekly number of drinking bouts estimated from GPS-collar data to the weekly number of drinking bouts estimated from audio loggers using linear regression.

Total time spent drinking is the product of drinking bout frequency and mean bout duration. Accordingly, we estimated mean total time spent drinking by kudu by multiplying the mean number of drinking bouts per week (calculated across monitored individuals within each week) by the mean bout length per week during the monitoring period (13 July–28 August 2021). We used linear regression to test for temporal trends in time spent drinking by kudu and to evaluate the relationship between mean distance to water and weekly time spent drinking.

***Additional statistical analyses*.**–We used general linear models (GLMs), weighted by sample RRA, to evaluate the effects of species and season on dietary water content. We included species (bushbuck or kudu), Julian day, and the corresponding 2-way interaction as explanatory variables. When the interaction was nonsignificant ($P > 0.10$), we removed it and refit the model with only main effects. As a complementary analysis, we categorized plant species according to whether preformed water content differed between the early and late dry seasons, as determined using ANOVA ($\alpha = 0.10$). We then used 2-sample Z-tests to determine whether the proportional consumption of plant species in each category—that is, plants that either declined ('desiccators') or did not decline ('moisture retainers') in water content as the dry season progressed changed between the early and late dry seasons. We used GLMs to test for temporal trends in fecal water content as the dry season progressed and for differences in fecal water between species. We included species, Julian day, and their interaction as covariates (nonsignificant interactions were removed and models refit). To probe the basis of changes in preformed water content across the dry season we used linear regression to investigate relationships between seasonal percent water loss (early to late-dry season) and leaf mass per area (an expected correlate of evaporative water loss) and plant height (related to 'woodiness') of each key forage species.

RESULTS

Trends in plant water content.–Mean water content of measured food-plant taxa declined from 67.4% in the early dry season to 59.4% in the late dry season (ANOVA, $F_{2,78} = 5.52$, $P < 0.01$; Fig. 2). At the species level, water content declined between the early and late dry seasons in roughly half (54%) of measured plant taxa (Table A.1, Fig. A.1). For 'desiccator' taxa, mean ± SD water content (by mass) was 70.6 ± 8.1% in the early dry season and 58.3 ± 10.1% in the late dry season. For 'moisture-retaining' taxa, mean ± SD water content was 63.4 ± 5.8% during the early dry season and 60.8 ± 6.4% during the late dry season. The rate of water loss during the dry season was related to both leaf mass per area and plant height. Taller (woodier) plants and those with greater leaf mass per area lost less water between the early and late dry seasons (plant height: $\beta = -0.65$, $P = 0.04$, adj. $R^2 = 0.11$; leaf mass per area: $\beta = -0.09$, $P = 0.06$, adj. $R^2 = 0.10$; Fig. A.4).

Diet composition and water content.–Diet composition differed between bushbuck and kudu ($P < 0.001$, $R^2 = 0.071$) and also changed seasonally within species over time ($P \leq 0.06$ for all within-species comparisons; Fig. A.5). Preformed water content of bushbuck and kudu diets declined at similar rates as the dry season progressed ($\beta_{\mathrm{Julian}} = -0.06$, $P < 0.01$, adj. $R^2 = 0.19$; $n_{bushbuck} = 18$, $n_{kudu} = 55$; Fig. 3), and bushbuck diets contained marginally more preformed water than kudu diets ($\beta_{\mathrm{Kudu}} = -8.18$, $P = 0.14$; Fig. 3). Results of this analysis were nearly identical to those derived using a much larger dataset spanning 9 years of the ASHAMED project ($\beta_{\mathrm{Julian}} = -0.07$, $P < 0.01$; $\beta_{\mathrm{Kudu}} = -5.1$, $P < 0.01$; adj. $R^2 = 0.23$; Fig. 3). Fecal water content likewise declined at similar rates for both species ($\beta_{\mathrm{Julian}} = -0.12$, $P < 0.01$, adj. $R^2 = 0.39$; Fig. 3) and was if anything marginally higher for bushbuck than kudu ($\beta_{\mathrm{Kudu}} = -7.1$, $P = 0.14$).

As the dry season progressed, both antelope species shifted their diets toward plants that contained relatively more preformed water. During the early dry season, plants that were highly labile in water content (i.e., the ‘desiccators’, including many herbaceous and thin-leaved taxa) comprised a greater proportion ($P < 0.01$) of bushbuck diets than ‘moisture-retaining’ taxa (Table A.1, Fig. 4). In the late dry season, however, bushbuck shifted to consuming a significantly ($P < 0.01$) greater proportion of moisture-retaining plants (Table A.1, Fig. 4). Kudu diet composition was unrelated to plant water content early in the dry season ($P = 0.36$), but, similar to bushbuck, kudu shifted to consuming a greater proportion ($P < 0.01$) of moisture-retaining plants in the late dry season (Table A.1, Fig. 4).

***Selection for surface water*.–**Bushbuck and kudu both showed strong selection for surface water throughout the dry season (standardized coefficients; bushbuck: $\beta = -0.33$, $P < 0.01$; kudu: $\beta = -0.22$, $P < 0.01$). As the dry season progressed, however, we observed temporal changes in selection for surface water that differed between bushbuck and kudu. Bushbuck selected surface water more strongly ($\beta = -0.06$, $P < 0.01$, adj. $R^2 = 0.78$), whereas strength of selection for surface water by kudu declined later in the dry season ($\beta = 0.02$, $P < 0.01$, adj. $R^2 = 0.51$; Fig. 5).

***Surface-water consumption*.–**Mean duration of drinking bouts for kudu was 29.7 ± 2.6 s, and drinking bout duration did not change during 7 weeks of audio recordings ($\beta = -0.02$, $P = 0.97$, adj. $R^2 < 0.01$). Audio monitoring also indicated that the mean number of drinking bouts per week did not change ($\bar{x} = 3.29 \pm 0.4$ drinking bouts/week; $\beta_{Week} = 0.20$, $P = 0.30$, adj. $R^2 = 0.05$). The relationship between mean number of weekly drinking bouts recorded sonically and mean number of weekly drinking bouts estimated from GPS data (Table A.2) during the same period was positive and significant ($\beta = 0.40$, $P = 0.04$, adj. $R^2 = 0.54$), suggesting that both audio loggers and GPS tracking of movements are effective means of identifying instances of drinking. Additionally, time spent drinking each week was inversely related to mean distance to water ($\beta = -0.43$, $P = 0.03$, adj. $R^2 = 0.14$), suggesting that proximity to water may indeed be a useful proxy for surface-water dependence. Total time spent drinking by kudu averaged 98 ± 30 s/week, and did not change across the 7 weeks of audio monitoring ($\beta = 0.82$, $P = 0.40$; Fig. 6).

DISCUSSION

We tested the hypotheses that browsing antelopes would respond to declining plant water content during the dry season by adjusting their diets, and that the consequences of those adjustments would differ between species owing to physiological traits and requirements that scale with body size. The composition of bushbuck and kudu diets changed significantly as the dry season progressed, supporting our first hypothesis. For both species, shifts in diet closely tracked changes in plant water content, reducing (yet failing to prevent) declines in dietary water intake. These results underscore the importance of preformed water to savanna herbivores and suggest a need to better understand the role of water requirements and associated hydration strategies in regulating the dynamics of large-herbivore communities.

Although we observed differences in diet composition and habitat selection between bushbuck and kudu, those differences often were not in the direction we expected. Proportional consumption of preformed water was comparable between bushbuck and kudu, but kudu, the larger of the two species by ~4-fold, relaxed their selection for surface water as the dry season progressed and exhibited no change in time spent drinking. In contrast, bushbuck exhibited stronger selection for surface water later in the dry season. One potential explanation for these results is that the significant reduction in fecal water loss exhibited by both species was sufficient to prevent kudu from needing to increase surface water consumption late in the dry season, but was not sufficient for bushbuck. Although we observed only a marginal difference in fecal water content between these species in our study, data summarized by Veldhuis et al. (2019) suggest that kudu have a greater ability to reduce fecal water content than bushbuck, lending credence to this hypothesis. Interspecific differences in urine osmolality and/or volume (Cain et al., 2006) also could have contributed to the difference in surface-water dependence we observed. Regardless of the underlying mechanisms, our results indicate that bushbuck are more dependent on surface water than kudu, refuting our interspecific predictions and supporting the proposition that body size alone is insufficient for predicting surface water dependence of species in diverse large-herbivore communities (Veldhuis et al. 2019).

One limitation of our study stemmed from the shifting diets of antelope, and of bushbuck in particular, as the dry season progressed. Previous data on *Tragelaphus* spp. diets in Gorongosa have been collected largely during the mid- to late-dry season. One consequence of using those data to generate our plant species list for sampling preformed water content was that those species sometimes comprised <50% (our threshold for inclusion in diet-based analyses) of sampled diets during the early dry season. This limited our early dry season sample size for bushbuck and reduced our ability to detect temporal changes in the water content of bushbuck diets. Nevertheless, that we did still detect significant changes in dietary water content in bushbuck, and that our comparable analysis of the larger ASHAMED dataset recapitulated these results, suggest that our conclusions are robust to this limitation. More broadly, our results suggest that future studies should not take for granted that diet composition and associated dietary traits are invariant even with a season, and that longitudinal sampling of diets (e.g., Walker et al., 2023a) has considerable potential to shed new light on the nuanced causes and consequences of dietary variation within and among species. Another limitation of our study is that we did not have data on relationships between plant water or nutrient content and proximity to surface water. If plants closer to surface water contained more nutrients, then the patterns of surface water selection we observed may have been influenced more by nutritional requirements than by the need to drink. Rigorously testing for this will require systematic sampling of foliage of a mix of plant species across field-measured gradients of proximity to surface water.

Africa is one of the most vulnerable parts of the world to climate change (Serdeczny et al., 2017), and a thorough understanding of how large herbivores are likely to cope with such changes is imperative for predicting population- and community-level responses (Fuller et al., 2016). Like much of the continent, Gorongosa is projected to become hotter and drier over the next century (IPCC 2022), and changes in the distribution and availability of surface water will likely have strong effects on Africa's diverse large-herbivores communities. As obligate browsers, bushbuck and kudu are often considered to be surface-water independent (Kihwele et al., 2020). Our results demonstrate, however, that considerable variation in surface water dependence exists even within this guild, let alone across the browser-grazer continuum. This variation has likely been underappreciated owing to the technical challenges of quantifying drinking behavior in free-ranging large herbivores. Nevertheless, interspecific differences in surface water dependence could have important effects on the distribution and composition of large-herbivore communities as temperatures warm and droughts become more frequent and severe. For example, a hotter, drier climate is likely to intensify the tradeoff between water requirements and predation risk for species like bushbuck that are both smaller and more water dependent. Body size scales inversely with predation risk (Hopcraft et al., 2010; Sinclair et al., 2003), and thus smaller species that also depend more heavily on surface water are likely to experience increased predation as surface water becomes less available and individuals are forced to concentrate their activity around remaining water sources (Mosser et al., 2009; Veldhuis et al., 2019). Alternatively, because the ability to dissipate excess heat also scales inversely with body size (owing to the smaller surface-area-to-volume ratios and thicker boundary layers that typify larger animals; Porter & Gates, 1969; Speakman & Król, 2010), warming temperatures could increase the hydric costs of thermoregulation disproportionately more in larger-bodied species. This could, in turn, increase surface water dependence of larger species, a trend that would be particularly consequential for large grazers that are already heavily dependent on surface water. Disentangling and predicting such effects at the population and community levels will require mechanistic approaches that are grounded in the principles and concepts of physiology and behavior and that take full advantage of current tools and techniques for measuring animal responses to environmental variation. Our study takes an important step in that direction and provides both a conceptual and methodological basis for future efforts to more fully characterize variation in surface water dependence among large-herbivore species.

Data Availability

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.w0vt4b936 (Van Driessche et al., 2025).

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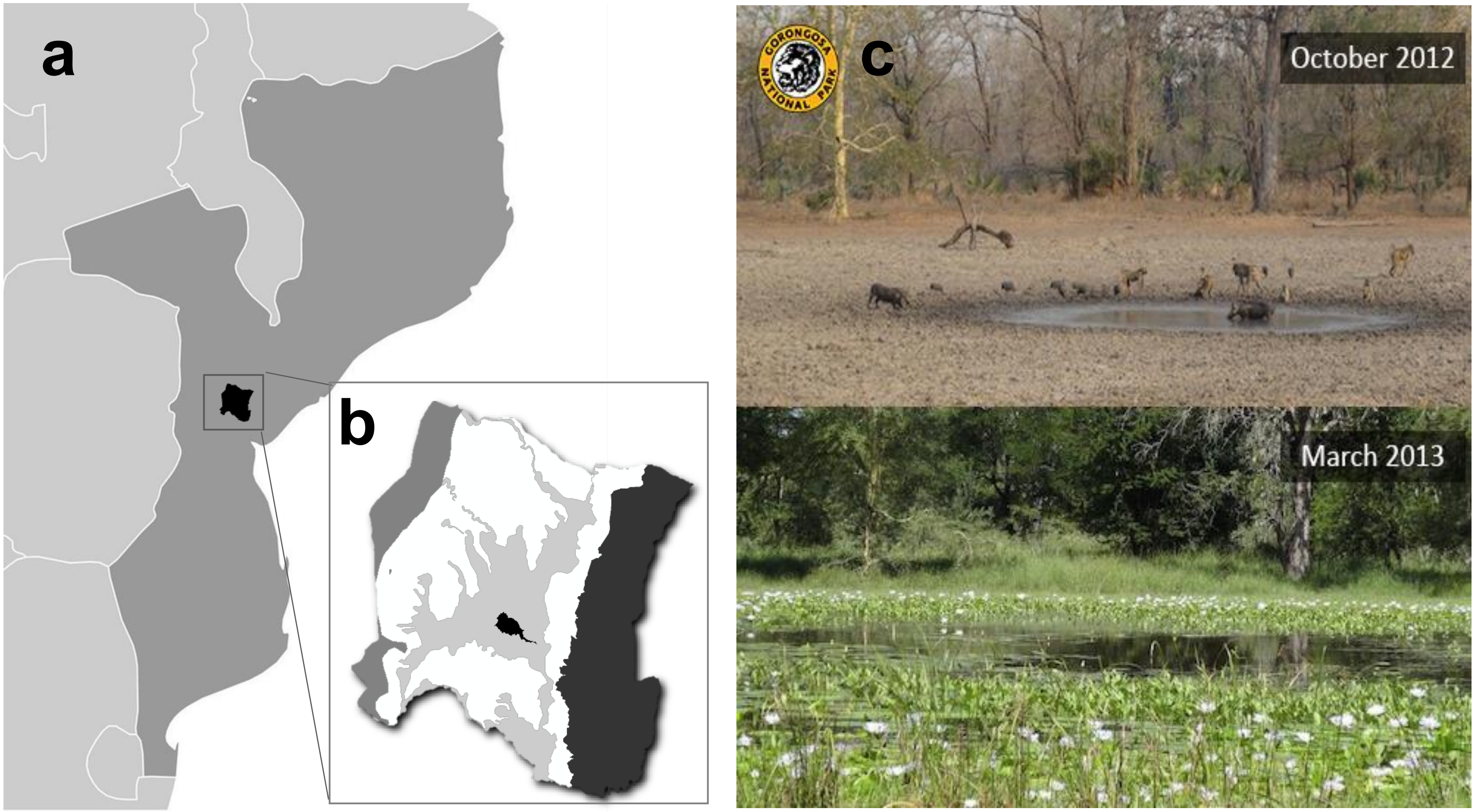

Figure 1. – (a) Gorongosa National Park is located in central Mozambique and (b) consists of four major habitat zones (from left: western escarpment [medium gray], woodland [white], floodplain [light gray], and eastern escarpment [dark gray], as well as Lake Urema [black]). (c) A perennial pan during the dry (October) and wet (March) seasons in Gorongosa. Photo used with permission from Gorongosa National Park.

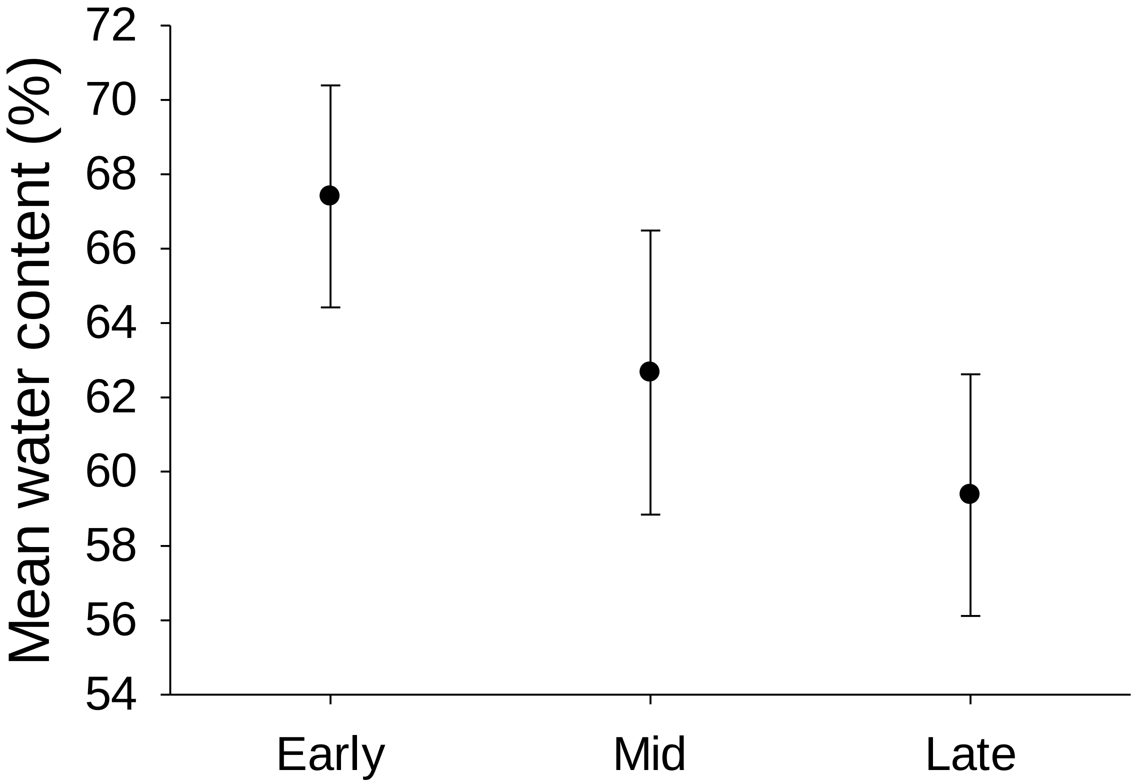

Figure 2. – Mean (±95% CI) preformed water content of plant species commonly consumed by bushbuck and kudu (Table A.1, Fig. A.1) in Gorongosa National Park, Mozambique during the dry season. Green leaves and stems (petioles) from 3 different individuals of each plant species were collected in July (mid dry) and October (late dry), 2021 and May (early dry), 2022.

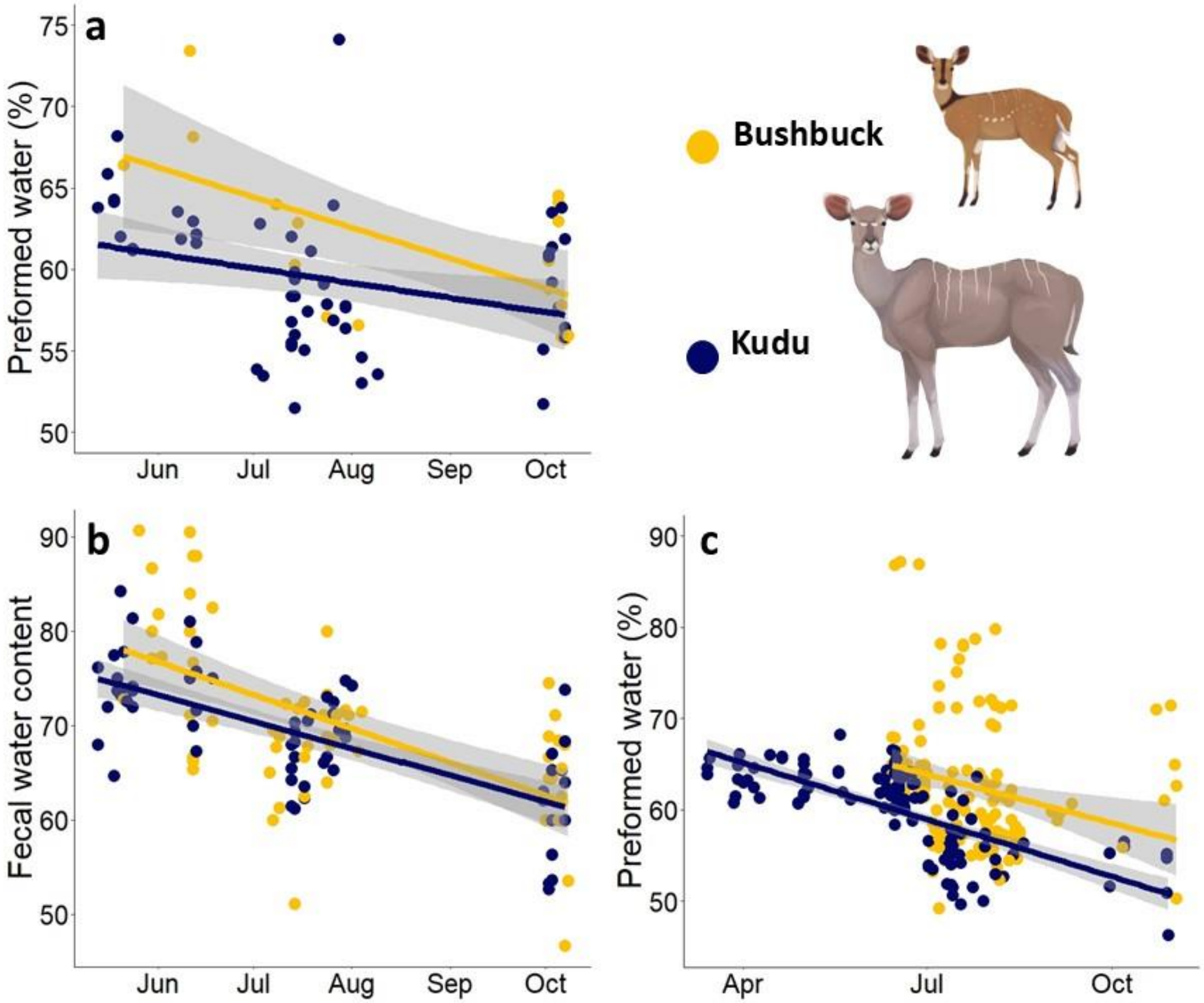

Figure 3. – Temporal trends in dietary and fecal water content of bushbuck and kudu in Gorongosa National Park, Mozambique during the dry season. (a) Preformed water in the diets of bushbuck (*n* = 18) and kudu (*n* = 55) declined significantly during the dry season

(β_{Julian} = -0.06, $P < 0.01$, adj. $R^2 = 0.19$) but differed only marginally between species ($\beta_{Species}$ = -8.18, $P = 0.14$). (b) Water content (percentage by mass) of bushbuck (*n* = 62, yellow) and kudu (*n* = 65, blue) fecal samples collected during the dry season in Gorongosa National Park, Mozambique. Early dry season fecal samples were collected in May and June 2022; mid-dry season samples were collected in July and August 2021; late-dry season samples were collected in September and October 2021. Fecal water content declined across the dry season for both species (β_{Julian} = -0.12, $P < 0.01$, adj. $R^2 = 0.39$) and was marginally higher for bushbuck than kudu (β_{Kudu} = -7.1, $P = 0.14$). (c) Preformed water in the diets of bushbuck (*n* = 145) and kudu (*n* = 124) estimated from fecal samples collected by the ASHAMED project, 2014–2022 (RRA ≥ 80%). Dietary water declined significantly during the dry season (β_{Julian} = -0.07, $P < 0.01$, adj. $R^2 = 0.23$), and bushbuck diets contained more water than kudu diets ($\beta_{Species}$ = -5.11, $P <$ 0.01).

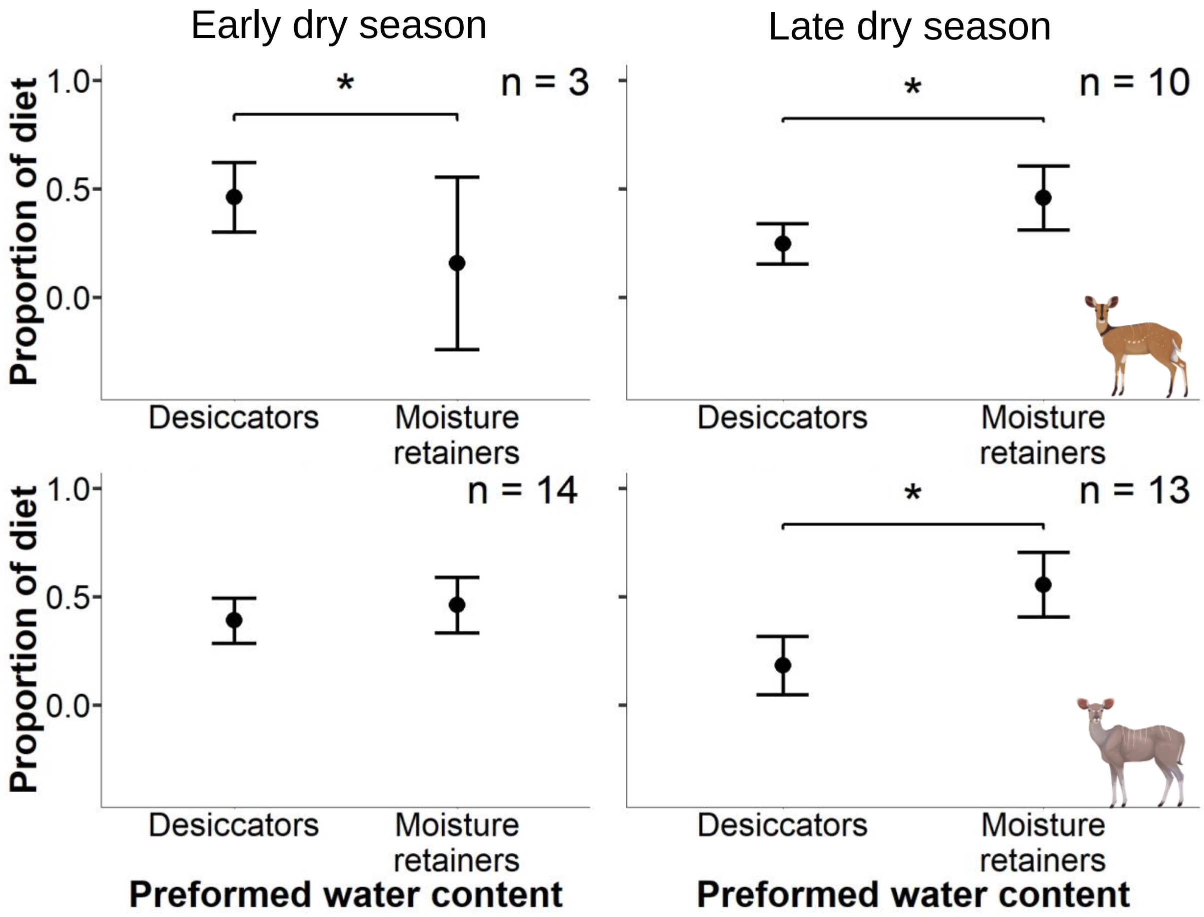

Figure 4. – Mean (± 95% CI) proportion of bushbuck (top row) and kudu (bottom row) diets consisting of plants with differing levels of preformed water content. Panels in the first column show results from the early dry season (May–June) and panels in the second column show results from the late dry season (September–October). Plants were categorized based on whether their water content did (Desiccators) or did not (Water retainers) decline as the dry season progressed (Table A.1, Fig. A.1). Significant differences in diet composition (two-sample z-test, α = 0.10) are indicated by an *.

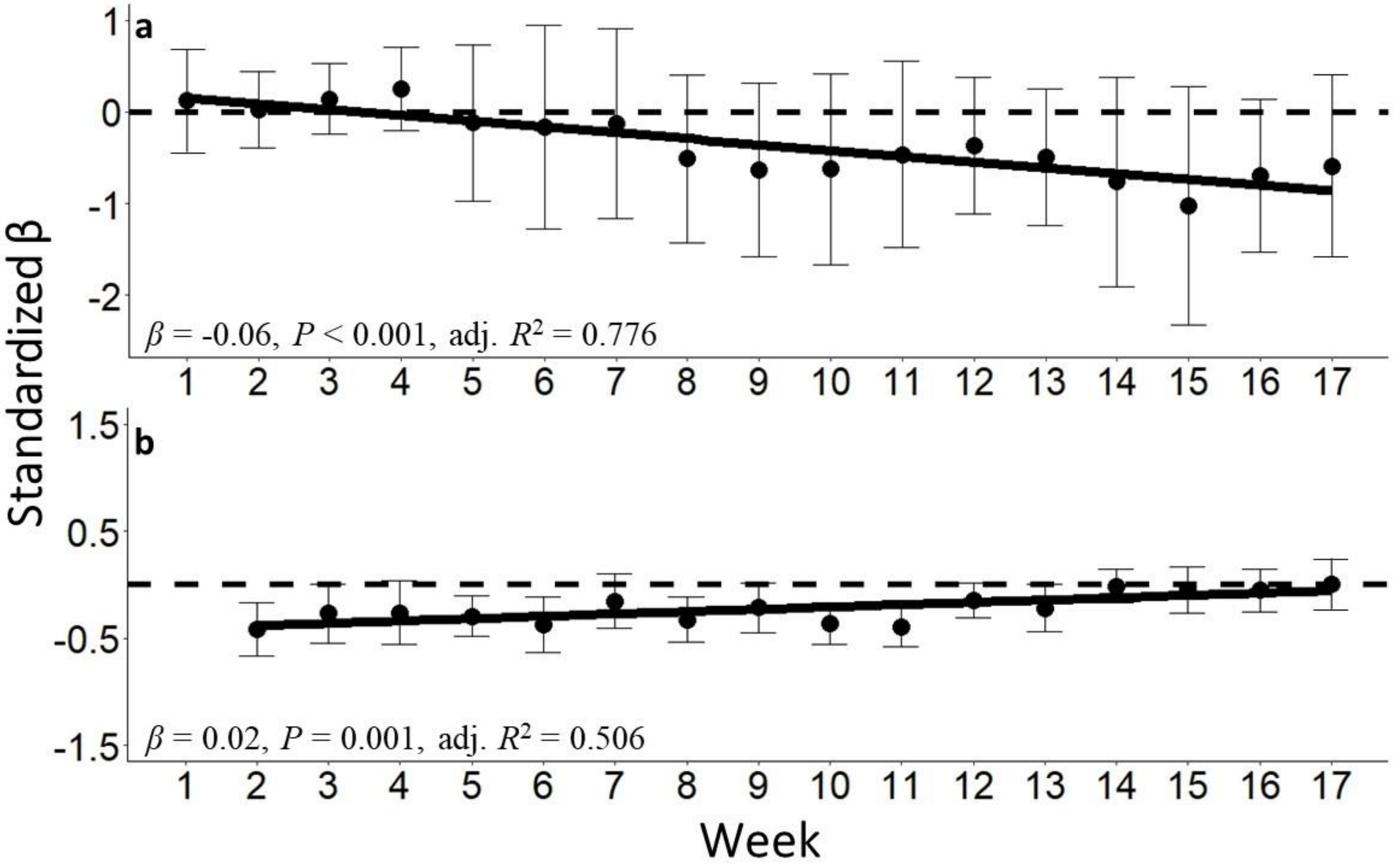

Figure 5 – Simple linear regressions, weighted by the inverse of the *SE* for each coefficient, of weekly changes in selection for surface water (standardized coefficient from GLMM) by (a) bushbuck and (b) kudu in Gorongosa National Park, Mozambique during 5 July–31 October, 2021. Strength of selection for surface water changed significantly during the dry season for both species, but in opposite

directions. Because the covariate was a distance metric (i.e., distance to surface water), more negative coefficients indicate stronger selection for surface water.

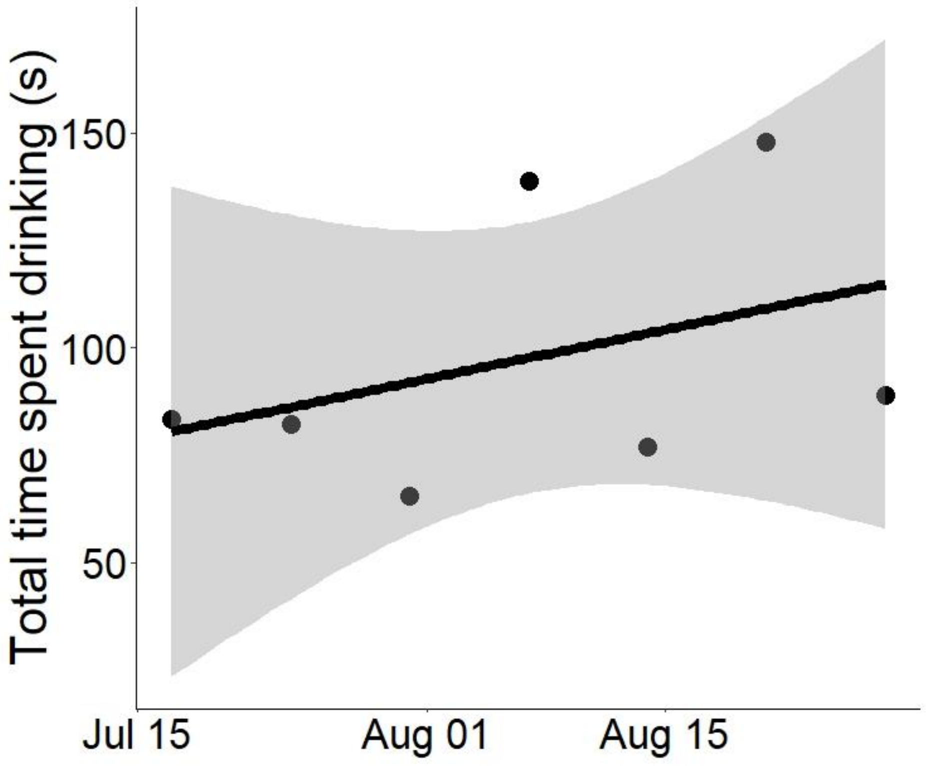

Figure 6. – Mean (± 95% CI) predicted time spent drinking per week by kudu (*n* = 3–7 individuals/week) during July–August in Gorongosa National Park, Mozambique. Estimates were obtained by multiplying the mean number of drinking bouts per week (calculated across monitored individuals within each week) by the mean bout length per week ($\beta_{\text{Julian}} = 0.82$, $P = 0.395$, adj. $R^2 < 0.01$).