

RESEARCH ARTICLE

Remote monitoring of short-term body mass variation in savanna ungulates

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Introduction

Animals inhabiting seasonal environments must deal with regular changes in climate, often associated with pulses of resource sparsity and availability. Seasonal variation in precipitation in particular can lead to changes in water availability and green vegetation, both critical resources

Abstract

Large herbivores in seasonal environments often experience mass variation due to temporal changes in the availability of critical resources like water and forage, as well as due to breeding events. Yet the documentation of mass variation in mammals of highly seasonal savanna habitats, which host the highest densities of grazing ungulates globally, has rarely been explored. Here, we showcase a method to evaluate seasonal mass variation in bovinds. Our method used mineral-baited scales and camera traps to enable us to track the body mass of three species through a period of wet and dry seasons in a South African savanna ecosystem. To illustrate one potential application of the method, we related body mass data to time, weather and resource availability. This showed that individuals altered their body masses markedly between seasons with, for example, female Kudu (*Tragelaphus strepsiceros*) gaining, on average, > 21 kg over the 15-week wet-season period in 1 year. These changes were positively related to factors such as vegetation productivity (assessed using NDVI) and the frequency of rains. This method enables easy, non-lethal and non-invasive acquisition of mass data. The equipment is easy to deploy concurrently over large areas. Monitoring by this method has a variety of possible applications, potentially providing a useful early-warning indicator of body condition to inform management, or providing information about ecological states, such as parturition or the reproductive effort of males. Given the longer and harsher dry seasons experienced in many arid systems in recent decades, and projected in future, this method may provide a straightforward means of monitoring long-term body condition in animals as a result of environmental change.

for large herbivores (Parker et al., 2009). Savanna ecosystems, which are typified by a hot, wet season and a cooler, dry season are common in subtropical regions. Seasonal water scarcity results in extensive grasslands with scattered trees, supporting very high densities of herbivores. To deal with resource scarcity and to maximize fitness, large herbivores inhabiting seasonally variable

environments often optimize energy expenditure by giving birth and mating when resources are abundant (Côté & Festa-Bianchet, 2001; Mason et al., 2012; Ogutu et al., 2015), and migrating when resources are scarce (Barker et al., 2019; Boyers et al., 2019, 2021; Debeffe et al., 2017; Spaan et al., 2019).

In general, body mass varies according to availability of resources (Kornél & Lanszki, 2017), with factors such as climate change also impacting individual condition and behaviour (Mason et al., 2014). Energy availability affects reproduction (Green et al., 2017; Newbolt et al., 2017), survival (Parker et al., 2009), behaviour (Brivio et al., 2014; Li, 2013), parasite load (Debeffe et al., 2016) and home range (Ofstad et al., 2016) of mammals. Despite the importance of nutritional state for individual fitness (Festa-Bianchet et al., 2019; Parker et al., 2009), short-term mass variation in animals inhabiting seasonal environments has been little studied. Studies that have explored these issues have focussed on body growth (e.g. Bergeron et al., 2010; Brambilla et al., 2018), long-term body size changes (Martin et al., 2018), and variation during reproduction (Therrien et al., 2007). Studies of seasonal changes of ungulate body mass often use data from hunted individuals, hence, repeated measures on individuals are impossible (Mason et al., 2012; Risco et al., 2018; Swanepoel et al., 2014). Some studies have used limited capturing and weighing of live animals (e.g., Lemaître et al., 2018; Newbolt et al., 2017). However, such studies are expensive and, thus, tend to be localized in better-resourced countries (e.g., red deer *Cervus elaphus* in the Isle of Rum, UK <https://rumdeer.bio.ed.ac.uk/>; Soay sheep *Ovis aries* in St Kilda, UK <https://soaysheep.bio.ed.ac.uk/>), and rarely describe the seasonal, short-term changes of body mass taking into account individual heterogeneity, because they usually cannot measure the same individuals repeatedly, at short-term intervals.

Monitoring seasonal variation in body mass can also provide valuable information about the state of herbivore populations, with the potential to provide an early-warning indicator of population collapse (Burant et al., 2021; Stephenson et al., 2020). Changes in mass provoke physiological changes in individuals (Desforges et al., 2020; Merems et al., 2020), which may alter population dynamics. Currently, changes in recruitment are most commonly used to predict population decline (Gailard et al., 1998). Body mass monitoring offers a means for site managers to respond to deteriorating conditions before the effects become manifest in population declines. In addition to the intra-annual periodicity of seasonal environments, ongoing anthropogenic climate change introduces a longer-term factor that might alter species' condition and, hence, mass (Burant et al., 2021; Middleton et al., 2018). Although the impacts of these

phenomena on large herbivores are uncertain, monitoring body mass changes may better prepare us for future events (Desforges et al., 2020; Pigeon et al., 2017).

Capturing and weighing individuals is the most accurate method to monitor body mass of large herbivores without hunting them (Bergman et al., 2018; Kautz et al., 2019). Nevertheless, it is costly to execute, stressful for animals, and has low success for repeatedly measuring individuals. Visual assessments of body condition, from direct encounters (Ezenwa et al., 2009) and camera trap images (Pérez-Flores et al., 2016; Smiley et al., 2020), permit remote and repeated mass estimation without manipulation. However, such assessments may differ between observers, making them subjective and highly inaccurate (Husin et al., 2012). Walk-on scales have been used to a limited extent to measure mass (as a proxy for condition) and are both objective and accurate (Bassano et al., 2003). However, to date, this method has been applied only to temperate and temperate-montane species with observers having to wait to manually observe the body mass of animals (e.g. Brambilla et al., 2018; Castro et al., 2018; Festa-Bianchet et al., 2019; Therrien et al., 2007). This approach is therefore costly in terms of person-hours and cannot provide continual, long-term surveillance. Cautious individuals, and nocturnal and crepuscular species are also likely to be under-recorded using this method.

Here, we use a novel method to explore the intra- and inter-annual changes in body mass of large herbivores, using several African ungulates as a case study, highlighting how mass changes can be linked to their annual life cycle events. We used walk-on scales (Bassano et al., 2003), baited with a mineral lick, and monitored with motion- and heat-triggered cameras to remotely weigh individual animals in a South African wildlife reserve. We hypothesized that body mass would vary seasonally, being positively related to changing availability of forage and water. We discuss the importance of monitoring mass variation in seasonal environments, and the potential utility of this technique for both managers and researchers.

Materials and Methods

Study site and species

The research was conducted at a 3875 ha game reserve located in the South African arid savanna near Pilanesberg National Park in Northwest Province (25°15'43"S 27° 5'4"E). The reserve supports 18 ungulate species, which are principally managed for conservation and research purposes (Table S1). Ungulate density is maintained below their carrying capacity by low-intensity hunting and commercial capture of a few species. Natural predation by larger predators is low (leopard *Panthera*

pardus is the largest predator within the reserve, though only an irregular visitor; caracal *Caracal caracal* is resident and the only other predator likely to take ungulates, hunting animals up to the size of Impala *Aepyceros melampus* [circa 45 kg]). Other large predators that occur in protected areas in the region, such as lion *Panthera leo*, cheetah *Acinonyx jubatus*, wild dog *Lycaon pictus* and spotted hyaena *Crocuta crocuta*, are absent from the site. A 3 m electrified perimeter fence around the site restricts ungulate movements in and out of the reserve. The reserve mainly comprises savanna grasslands, which covers 83% of its surface. The remainder is made up of woodland, thicket, and water bodies, including several artificial water points. Rain typically falls from October to mid-May, after which there is little or no rain until the following October. During the current project, the dry season extended from 15th May to 4th October in 2017, and from 15th May to 30th September in 2018 (from rainfall gauges on site, Fig. 1A). Start and end of wet and dry seasons were defined by intensity and frequency of daily rainfall. This regime promotes substantial seasonal changes in vegetation, which reaches its highest and lowest greenery levels during wet and dry seasons, respectively (Fig. 1B).

Our study species comprised three bovids that co-occur across sub-Saharan African savannas: blue wildebeest *Connochaetes taurinus*, greater kudu *Tragelaphus strepsiceros* and red hartebeest *Alcelaphus buselaphus*. We targeted these species as they were the most regular species (from previous camera trap data) to use the water holes close to the monitoring site. We excluded impala as a focal species, despite it occurring commonly at the monitoring sites, as, unlike the previous three species, individuals could not be reliably differentiated from each other. Wildebeest and hartebeest predominantly graze whilst kudu mainly browse. We focussed on adult individuals in this study to limit detected changes to seasonal variation, and avoiding recording mass changes associated with maturation-related juvenile growth.

In Southern Africa, breeding of all three species is seasonal, producing single calves. In wildebeest, calves are born after circa. And 250 days of gestation, during the middle of the wet season (Estes, 1976; Owen-Smith, 1993; Perrin, 1999; Spinage, 1973). In kudu, calves are typically born after 255 days, in the early wet season (Castelló et al., 2016; Estes, 1976; Owen-Smith, 1993; Perrin, 1999; Spinage, 1973). In red hartebeest, gestation is circa. And 240 days, with calving also focussed towards the end of

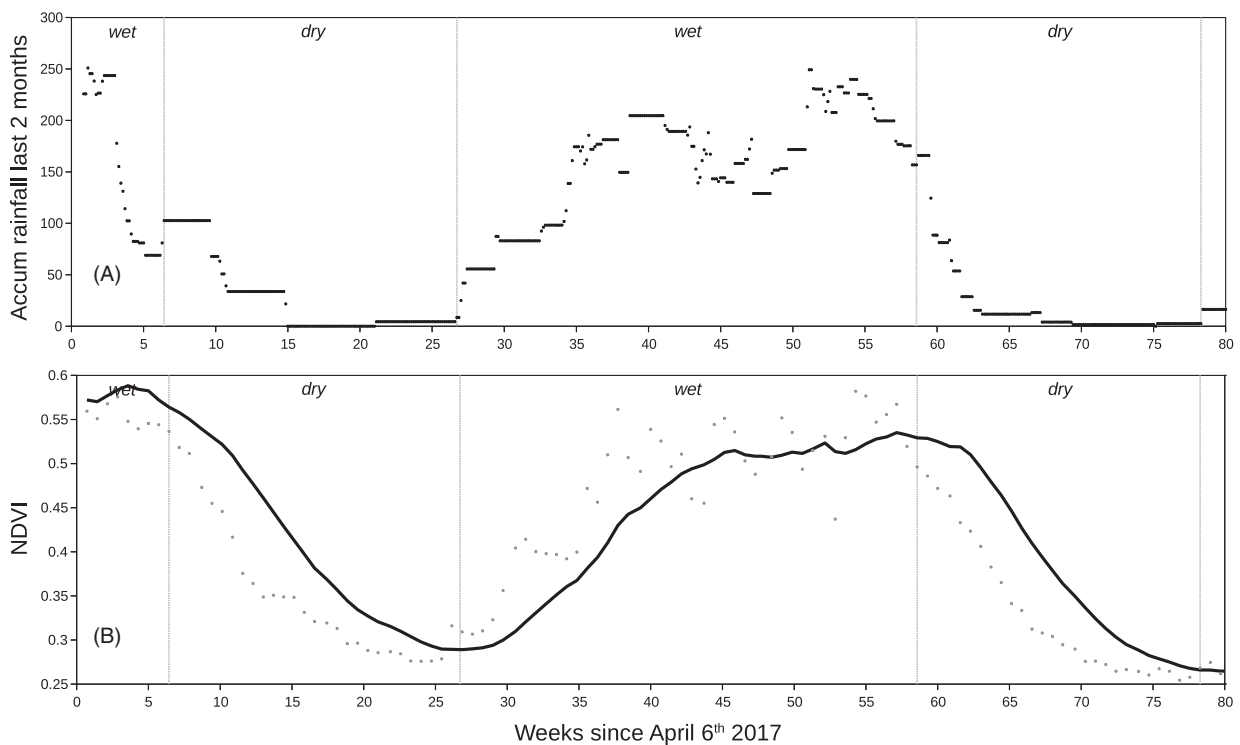


Figure 1. (A) Accumulated rainfall; black dots represent daily accumulated rainfall over the preceding last 60 days. (B) Mean grassland NDVI at MWR, where grey dots represent NDVI from the previous 5 days, and the black line represents average NDVI from the preceding 60 days (Santangeli et al., 2018). Vertical grey dotted lines represent starts/ends of wet and dry seasons.

the dry season (Castelló et al., 2016; Nowak, 1997; Skinner et al., 1974; Spinage, 1973).

Body mass and environmental data collection

Body mass data were collected between April 6th 2017 to October 8th 2018, using two walk-on weighing scales (range 0–3000 kg, accuracy ± 0.5 kg) that were deployed close to water-points (Fig. 2A). The setup comprised a 50 kg salt block to attract animals, a 1.5×1.5 m² metal platform scale (3-Ton Platform Scale LMI Ltd., <http://www.lmi.co.za/wordpress/>) with a linked display (LS4F Readout Instrument LMI Ltd), and a camera trap (Reconyx Hyperfire HC500) that captured photographs of animals along with their mass reading when using the scales (Fig. 2B). Scales were continuously powered by car batteries that were replaced and recharged every 2 weeks, at which point batteries and memory cards of camera traps were also checked. Car batteries were sealed inside closed containers to protect them from humidity, and surrounded by iron rods (80–100 cm high) that were hammered into the ground to keep animals away from them. Iron rods were also placed around the reader and the camera trap to prevent animals from damaging them and obstructing the view from the camera trap. Electric cables from platforms to mass readers and car batteries were enclosed in rubber hoses, buried underground and covered with rocks to protect them from animal biting and trampling. The four corners of the scale were supported on cement bricks that were buried to ground level to provide greater stability. Finally, each measuring station was surrounded by a 1–2 m wire fence (see Fig. 2B), reinforced with branches and trunks to increase visibility. The fence had only one entrance, and this directed animals to step on the scale in order to access the salt block. When more than one individual was on the platform individual masses were calculated by subtraction as individuals stepped off. We positioned the camera sensor and the reader screen so as to avoid direct sunlight. We further limited light interfering with LCD image by deployed cameras and mass readers under the shade of trees. Flash reflection on the mass reader was prevented by angling the reader at 20–40° to the camera (Fig. 2B).

For this individual-level exploration of body mass variation, we only considered data from individually identifiable animals. Although animals were not tagged, we focused on species and individuals that were easily distinguished from each other, during both day and night, by unique patterns in horn shape and hair length, and by scars on their face, ears, neck, legs, and feet (Fig. 2C). For individuals that could be uniquely identified, mass per week was calculated as the mean of all daily mass

readings from that individual. By averaging body mass per week, we aimed to reduce short-term variations, such as differences in body mass because of drinking water just before stepping on the scale. If the body mass was recorded more than once within a day, the mean mass for that day was used. Only adult individuals using the scales for a minimum period > 3 months, and with > 2 weeks of readings within a season, were included in the study. Also, juvenile markings were less distinct, so we were less confident in our ability to identify specific juveniles.

Normalized Difference of Vegetation Index (NDVI) was used as a proxy of availability of high-quality forage. NDVI provides a measure of photosynthetic activity, derived from satellite sensors (Pettorelli et al., 2005). And 109 satellite images were downloaded to cover the entire study period, obtained from the AQUA sensor eMODIS NDVI V6 (United States Geological Survey; <https://earthexplorer.usgs.gov/>). These comprised composite images of 250 m spatial resolution and are available on a 5-day cycle. As animals can forage freely across the reserve, we calculated the mean NDVI for grassland areas across the entire site. Only one image (21st February 2018) was discarded (following Agapiou et al., 2011) because $> 50\%$ of the pixels with grassland were corrupted by atmospheric conditions. Mean NDVI for the 30- (NDVI30) and 60-day (NDVI60) periods prior to a body mass reading (Santangeli et al., 2018) were calculated by averaging NDVI across all the images within the relevant period before a weighing event.

Accumulated rainfall for the 30- (RAIN30) and 60-day (RAIN60) periods prior to a weighing event along with the frequency of rainy events (number of days with precipitation) during last 30 (FRAIN30) and 60 days (FRAIN60) were used as indices of water availability (Santangeli et al., 2018). Daily rainfall (accuracy ± 1 mm per day) across the study area was obtained by averaging readings from five distributed rain gauges.

Data analysis

Hierarchical Generalized Additive Models (HGAMs, Pedersen et al., 2019) were used to relate weekly mass fluctuations to date, NDVI, and water availability, for each analysed group. Groups comprised uniquely identifiable individuals of the same species and sex. Within each group of animals (one sex of a given species), we standardized masses. The aim of this was to enhance visualization, putting the masses of all sexes and species on a common scale, whilst retaining the relative variation among individuals within each group. To standardize in this way, we began by calculating the mean mass of each individual in each week, based on all the measurements

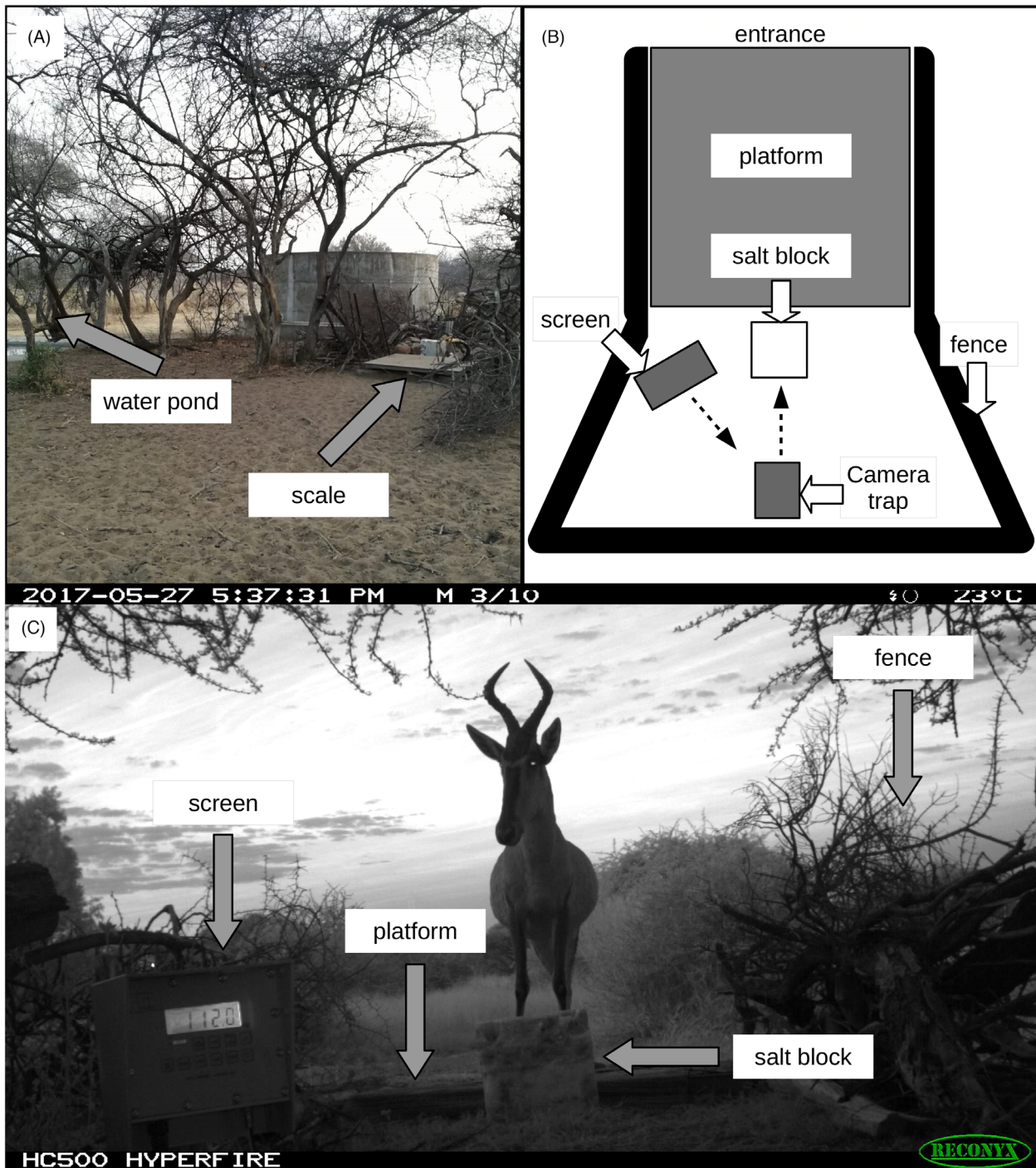


Figure 2. Body mass stations. (A) Location of one of the two scales next to an artificial pond, (B) Representation of the set-up from an aerial view, and (C) Example mass reading of a female red hartebeest that was attracted to the scale.

we had for that individual in the given week. We denote the mean mass of individual i in week w , $M_{i,w}$. For groups containing measurements for n individuals across W weeks, we estimated the mean weekly masses of all individuals, \underline{M} , as

$$\underline{M} = \frac{\sum_{i=1}^n \sum_{w=1}^W M_{i,w}}{nW}$$

The standardized mass, S , of individual i in week w was then

$$S_{i,w} = \frac{M_{i,w}}{\underline{M}}$$

Individual identifications were used as random intercepts to control for variability among individuals. Date was included as *weeks since April 6th 2017* (running from 1 to 79 weeks) to assess temporal variation of body mass across the entire study period as a time series. We do not expect the same body mass for the same date in different years because weather conditions and resource availability vary inter-annually. HGAMs included penalized thin-plate regression splines as smooth terms (Wood, 2003) for date, availability of fresh forage (weekly mean NDVI, and NDVI30 and NDVI60) and water availability (RAIN30, RAIN60, FRAIN30, FRAIN60).

We built models with only one smoother at a time, because when adding a second variable models presented concurvity issues (concurvity was > 0.5 ; Ramsay et al., 2003). Concurvity is non-linear collinearity that may bias predictions (Dominici et al., 2002). We ran two separate sets of models, each with a single smoother. All models assumed a Gaussian distribution with identity link functions, and the smoothing selection was defined by marginal likelihood (Wood, 2011, 2017). Model quality was checked using basis dimension assessments (BDAs; Wood, 2017) and visually inspecting plots of residuals, and plots of observed versus fitted values.

Two models were selected per group: (i) the first had a smoother for date, to explore temporal variation, and (ii) the second had a smoother for availability of resources (NDVI or precipitation), to explore seasonal variation of resources. We used Akaike Information Criterion (AIC; Akaike, 1974) to rank models; all models with $AIC \leq 2$ of the top model were considered equivalent (Burnham & Anderson, 2002). Of these, the model with highest explained deviance was selected to assess the effect of availability of resources on body mass. All analyses were performed using R version 3.5.2 (R Core Team, 2018), and the package 'mgcv' (Wood, 2019). Satellite images were processed using QGIS 3.4.6-Madeira (QGIS Development Team, 2019).

Results

Over the study period, 3700 body mass records were registered from 10 species (Fig. 3; information about additional species is reported as supporting information). Mass data for our three focal species were: blue wildebeest, $n = 435$; red hartebeest, $n = 503$; greater kudu, $n = 2383$. From those, 1838 records could be allocated to 58 individuals comprising: adult blue wildebeest ($n = 6$ females, 1 male), greater kudu ($n = 29$ females, 11 males) and red hartebeest ($n = 10$ females, 1

male). These latter individuals used the scales for between two and 38 weeks (mean number of recordings per individual = 31.7 ± 27.7). Discarded data corresponded to records from either immature (848 body mass records) or individually unidentifiable individuals (728 body mass records).

After averaging mass records for individuals with repeat captures, this left 609 weekly body mass records for further analysis (Table 1; Fig. 4). Male blue wildebeest and male red hartebeest records were discarded from the analysis as only one uniquely identifiable individual per species used the scale for more than 3 months (see Fig. 3). Data included in the analysis corresponded to 40 weekly records of female blue wildebeest (from week 7 to 61), 389 weekly records of female greater kudu (from week 1 to 79), 96 weekly records of female red hartebeest (from week 10 to 61), and 70 weekly records of male greater kudu (from week 7 to 79).

All models including a smoother for date were significant (Table S2 to Table S5) and had the lowest AIC within their groups (Table 2). Although animals started to gain weight just after the beginning of the rainy season, each species varied in the mean date of peak weight gain (Fig. 5). In terms of the role of resource availability in impacting weight, models containing NDVI60 (female blue wildebeest, greater kudu and red hartebeest) and FRAIN60 (male greater kudu) performed best at predicting body mass (Table 2; Tables S2–S5).

As can be seen from Figure 5, the species (and sexes for kudu) varied in their mass gain across seasons, with some evidence of mean weight gain between 2017 and 2018 (inter annual gain = 27.01 ± 5.07 kg for female wildebeest; 9.99 ± 1.66 kg for female kudu; 16.72 ± 9.55 kg for male kudu; see Supporting information section for a more detailed description of mass changes). There were also changes in female and male mass that were consistent with calving and breeding events respectively (see discussion for detail). In the best wildebeest and female kudu models there was a significant nonlinear relationship between body mass and NDVI60 (Fig. 5B,D respectively). By contrast, in the best male kudu model there was a significant positive linear relationship between body mass and FRAIN60 (Fig. 5F). Similarly to the other female groups, in the best female hartebeest model there was a significant relationship between body mass and NDVI60, but this was linear (Fig. 5H).

Discussion

We documented temporal variation of body mass in three arid savanna ungulates that were exposed to natural resource fluctuations over an 18-month period. The automated weighing approach we developed was applied

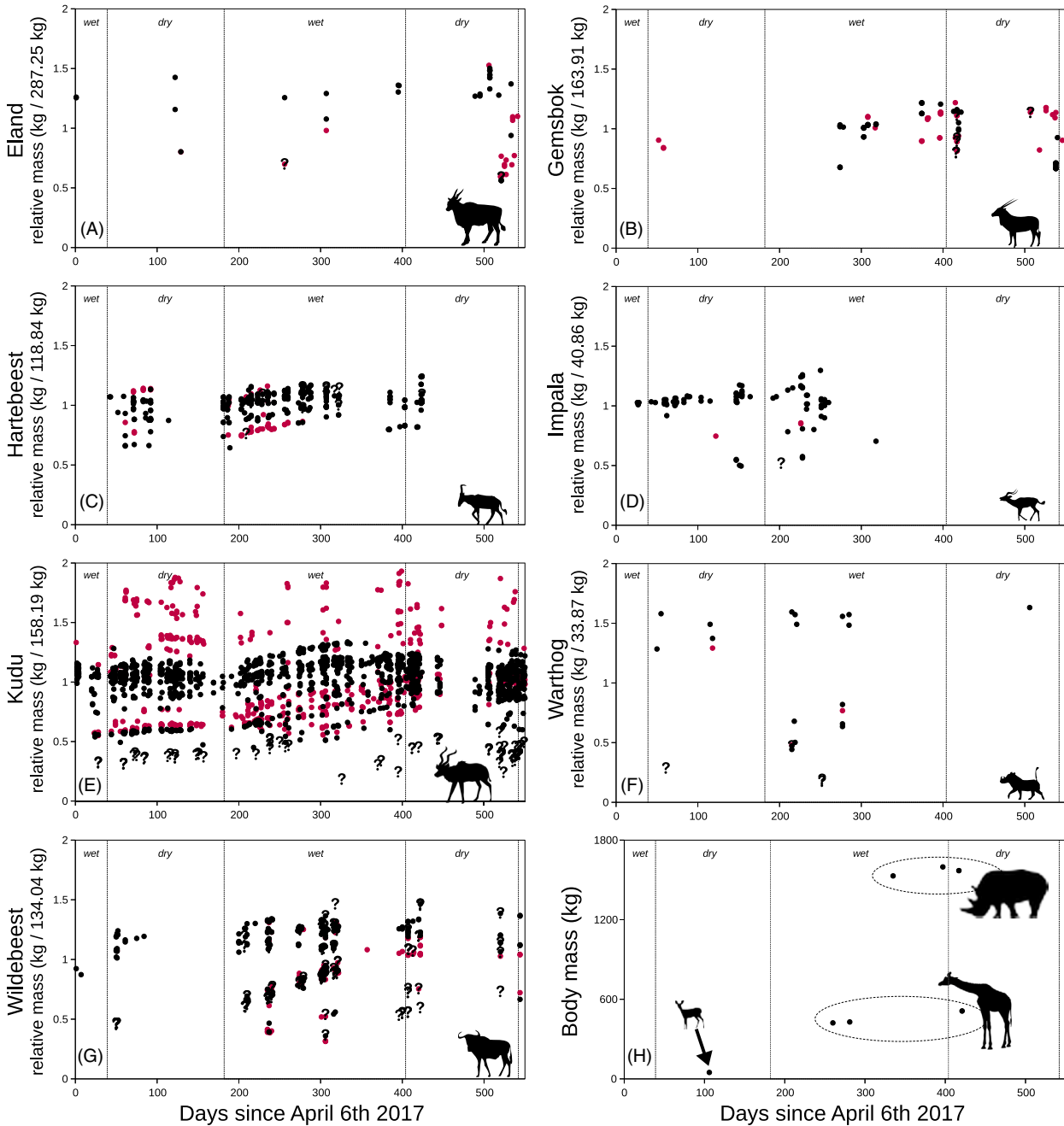


Figure 3. Total records of relative body mass in relation to the mean body mass of the species, where (A) shows data for eland, (B) gemsbok, (C) hartebeest, (D) impala, (E) kudu, (F) warthog, (G) wildebeest, and (H) shows specific body mass records for giraffe ($n=4$), reedbuck ($n=1$) and rhino ($n=4$). Black dots represent records from females, red dots records from males, and “question marks” represent records from “unidentified sex” individuals. Vertical grey lines represent starts/ends of wet and dry seasons.

successfully in this sub-tropical savanna system to monitor fine temporal scale mass change of the common ungulates that coexist there. Ours is the first study, to our knowledge, that has been able to track, and non-destructively analyse, the short-term variations of body mass in ungulates of the seasonal tropics. In all previous similar studies,

in temperate ecosystems, data recording had relied upon human observers being in situ. This is the first time, to our knowledge, that camera traps have been used to automate the data recording process. This increases the opportunities for data recording during periods when an observer may influence the data collection or when they

Table 1. Summary of body mass records.

Group	Individuals recorded/ included	Data recorded/ included	Range body mass (kg)	Ave \pm SD body mass (kg)	Ave \pm SD weeks per individual
Blue Wildebeest (F)	15/6	66/40	143.7–196.5	168.8 \pm 11	6.7 \pm 3.1
Greater Kudu (F)	49/29	448/389	121.8–209.9	166.3 \pm 17.4	13.4 \pm 8.3
Greater Kudu (M)	12/11	74/70	192.8–296.1	238.8 \pm 29.9	6.4 \pm 4.1
Red Hartebeest (F)	15/10	109/96	101.3–148	122.9 \pm 9.8	9.6 \pm 4.7

(F) and (M) refer to females and males, respectively. Ave \pm SD refers to mean \pm standard deviation. “Individuals recorded/included” refers to total individuals that were identified using the scale for more than 1 week during the study period/individuals that complied with minimum requirements for being included in the analysis. “Data recorded/included” refers to total observations of individuals recorded and individuals that were included in the analysis.

cannot be present (e.g. at night, in harsh or remote environments, during unfavourable weather, or when working with timid species). It also permits the continuous monitoring of the mass of individuals, and makes the method easy to deploy concurrently over multiple areas. The method may help managers to obtain more accurate data on, for example, the proportion of females giving birth at a site. This could be especially helpful for managers of rarely visited sites or for species that are difficult to observe, particularly when females are secretive with their calves, and given that offspring are often exposed to very early predation, which can mask true fecundity. Considering the high number of threatened herbivores in grassland systems alone (e.g. Ripple et al., 2016), the relevance of medium to large herbivores for the functioning of many ecosystems, their value to human societies (du Toit & Cumming, 1999), and the current projected climate changes across much of the world (e.g. Baker et al., 2015), a cost-effective method to evaluate environmental impacts on condition is timely. Additionally, monitoring seasonal short-term variation of body mass using this method can provide reliable, near daily information on the current condition of populations, aiding managers and researchers, and with the potential to act as an early-warning indicator of, for example, condition-induced mortality events (Scheffer et al., 2009).

Seasonal changes in body mass

All species experienced changes in body mass throughout the year, with mass declining during dry seasons and increasing during wet season, as predicted, though the patterns of intra-seasonal and inter-annual mass loss we recorded is the first such description to our knowledge. Although there are studies assessing seasonal changes in body mass of ungulates worldwide (e.g., effect of temperature on body mass of moose *Alces alces* in Norway, van

Beest & Milner, 2013; long-term mass change of Alpine chamois *Rupicapra rupicapra* in Italy, Mason et al., 2014; seasonal changes in bighorn sheep in Canada, Douhard et al., 2018; mass change and winter mortality of white-tailed deer in USA, Kautz et al., 2019), the few African studies to date have focused on describing seasonal variation as recorded from small numbers of hunted animals (common warthog *Phacochoerus africanus* in South Africa, Swanepoel et al., 2014; black wildebeest *Connochaetus gnou* in South Africa, Hoffman et al., 2009), and masses were allocated only to season of hunting. Two further studies were found on seasonal mass changes of alive animals in Africa, focussing on small and medium sized African mammals (Madagascan roussette *Rousettus madagascariensis* [50–70 g] Goodman et al., 2017; and Egyptian mongoose *Herpestes ichneumon* [1.8–1.9 kg] Bandeira et al., 2019). Despite these latter studies being on a frugivore and omnivore respectively, their findings tend to match with the patterns of mass change that we report here. Individuals reached their minimum body mass at the end of the dry season, when availability of high-nutritious green vegetation also fell to a minimum (Fig. 1B). In our system, we typically recorded losses of 3% to 8% of body mass loss during the harsher dry season. These losses were considerably lower than the typical 15% to 30% losses in body mass measured in wild ungulates inhabiting other seasonal environments, such as montane (Japanese serow *Capricornis crispus*, Miura & Maruyama, 1986; mountain goat Festa-Bianchet & Côté, 2008) and arctic environments (black-tailed deer *Odocoileus hemionus sitkensis*, Parker et al., 1993; barren-ground caribou *Rangifer tarandus granti*, Allaye Chan-McLeod et al., 1999). This was slightly surprising, considering the climatic stochasticity of African savannas, where episodic extreme droughts can cause mass mortality (Veldhuis et al., 2019). We propose that to better understand seasonal and interannual mass changes in savanna

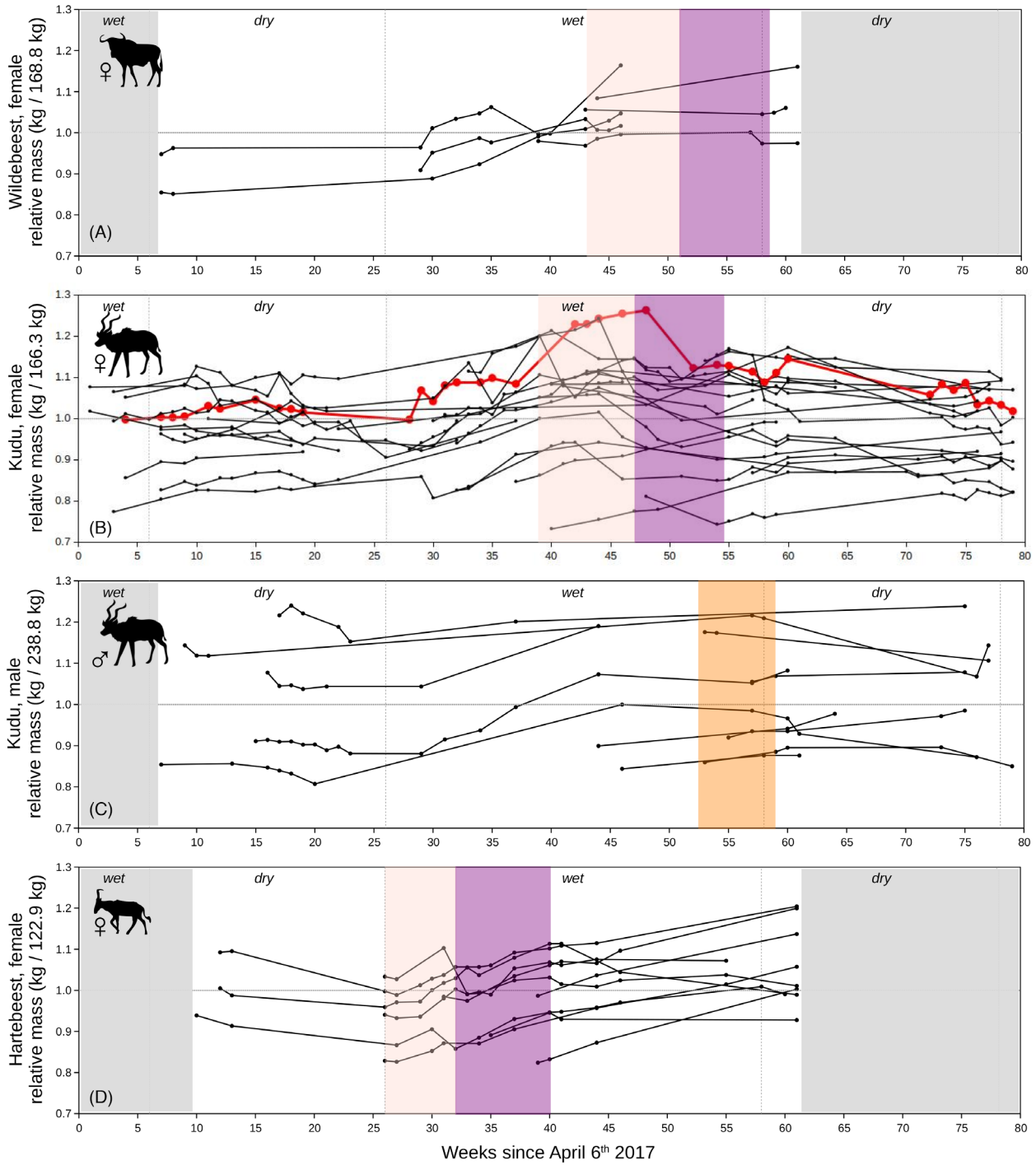


Figure 4. Fluctuations of the relative body mass in relation to the mean body mass of the group, where (A) shows female blue wildebeest, (B) female greater kudu, (C) male greater kudu, and (D) female red hartebeest. Black dots and lines to distinguish individual trends. Red dot and lines shows the specific trends of one female greater kudu. Vertical grey lines represent starts/ends of wet and dry seasons, and horizontal grey lines represent the group mean. Grey areas visualize weeks beyond the first and last records for each group. Peach areas visualize when calving peaks typically occurs for each species (Estes, 1976; Nowak, 1997; Perrin, 1999; Spinage, 1973), purple areas visualize when heavy lactation period typically occurs for each species (Ayotte et al., 2019), and orange area in male greater kudu plot visualizes when the peak of mating season may be occurring (Castelló et al., 2016).

Table 2. Models fitted per group.

Group	Predictors	DE (%)	edf	Δ AIC
Blue Wildebeest (F)	s(week)	83.1	3.01	0.00
	s(NDVI60)	85.1	5.96	0.00
	s(FRAIN30)	54.8	1	33.59
	s(ndvi 5 days)	57.9	3.62	36.97
	s(RAIN60)	49.9	1	37.68
	s(NDVI30)	52.4	2.17	38.61
	s(RAIN30)	46.6	1	40.15
Greater Kudu (F)	s(week)	85.2	8.09	0.00
	s(RAIN60)	did not passed BDAs		
	s(NDVI60)	80.8	4.24	21.11
	s(NDVI30)	80.6	4.95	27.87
	s(FRAIN60)	79.2	1	43.46
	s(ndvi 5 days)	79.6	3.23	43.90
	s(RAIN30)	77.7	2.49	75.97
Greater Kudu (M)	s(week)	95.9	6.03	0.00
	s(NDVI30)	did not passed BDAs		
	s(ndvi 5 days)	did not passed BDAs		
	s(NDVI60)	did not passed BDAs		
	s(FRAIN60)	88	1	6.50
	s(RAIN60)	87.9	1	7.43
	s(FRAIN30)	85.7	1	19.09
Red Hartebeest (F)	s(week)	80.8	3.86	0.00
	s(NDVI60)	77.7	1	0.00
	s(NDVI30)	76.8	1	3.87
	s(ndvi 5 days)	77.5	4.78	10.80
	s(RAIN30)	70.4	6.84	40.02
	s(FRAIN30)	64.4	4.93	54.79
	s(RAIN60)	58.7	1	58.59
s(FRAIN60)	58.2	1	59.74	

Models are organized from lowest to highest AIC. Bold text indicates the two selected models per group. "Predictor" indicates smoother included in the model, "DE" is deviance explained, "edf" is effective degrees of freedom, and " Δ AIC" is the difference with the model of lowest AIC. Grey rows indicate models with a smoother that did not pass the basis dimension assessments (BDAs), therefore were not considered for analysis.

species a longer-term monitoring program is needed to determine whether the mass changes reported here are representative for these dryland systems. The remote monitoring methods we describe in this paper would be well-suited to answer such questions.

Animals lose weight during unfavourable seasons in part because the harsh weather conditions and the scarcity of resources (Bonardi et al., 2017; Chang & Wiebe, 2016; Lesage et al., 2001) mean they burn more calories than they are able to acquire (Wato et al., 2016; Young & van Aarde, 2010). Unfortunately, this study cannot quantify whether any mass losses recorded were driven predominantly by loss of energy owing to harsh

weather conditions (e.g. very low or very high temperatures), or by scarce resources. One factor confounding such a generalization is the fact that, at the study site, animals were likely also influenced by the anthropogenic control of ungulate density (*via* the hunting and sale of animals) that maintained populations below their carrying capacity on the reserve (Bonardi et al., 2017; Delciellos et al., 2018; Ogutu et al., 2012).

In our study system, although blue wildebeest and greater kudu gained mass during the wet season, they did not increase body mass continually, which is likely explained by reproductive events. The timing and duration of wet-season weight stasis in females of these two species match with typical calving periods, which occurs at the middle/second half of the wet season in Southern Africa (Estes, 1976; Owen-Smith, 1993; Perrin, 1999; Spinage, 1973), and aftercare (intensive lactation typically occurs for 6–10 weeks after birth, Kingdon & Hoffmann, 2013). This, in turn, is suggestive of the species timing their calving to coincide with peak foraging conditions to avoid losing condition. Elsewhere, mass loss during the wet season has been associated with physiological costs of reproduction (Ayotte et al., 2019; Borowske et al., 2018; Festa-Bianchet et al., 2019), because in seasonal environments animals tend to give birth at the beginning of, or during the favourable season (Berkeley & Linklater, 2010; Cucco & Bowman, 2018; Ogutu et al., 2013, 2015), and they continue losing weight because of maternal care (Ayotte et al., 2019). The modelled declines in body mass of female blue wildebeest and greater kudu when NDVI60 exceeded 0.5 were likely influenced by the NDVI values reported at the start of the study period (dry season 2017; Fig. 1, as this was the only period when NDVI values passed this threshold). This may reflect some environmental impacts that preceded our period of monitoring affecting the mass of these species (e.g. prolonged or harsh dry period in the period leading up to the 2017 wet season). This could also explain the increase in mean mass across all species between successive dry seasons. Alternatively, these year-on-year increases may, in part, be driven by natural maturity of individuals. Environmental data from the study area, namely reduced precipitation and lower NDVI throughout the wet season of 2018 compared to 2017, hint that body mass change in these groups may be more related to body growth than availability of resources. The above suggests that a longer period of study, which controls for maturation mass increases, will be needed to elucidate long-term trends. Studies on montane ungulates have demonstrated continued mass gain from birth to adulthood, after which mass gain may continue at a lower rate until senescence, [e.g. bighorn sheep (Bérubé et al., 1999; Nussey et al., 2011; Pelletier & Festa-

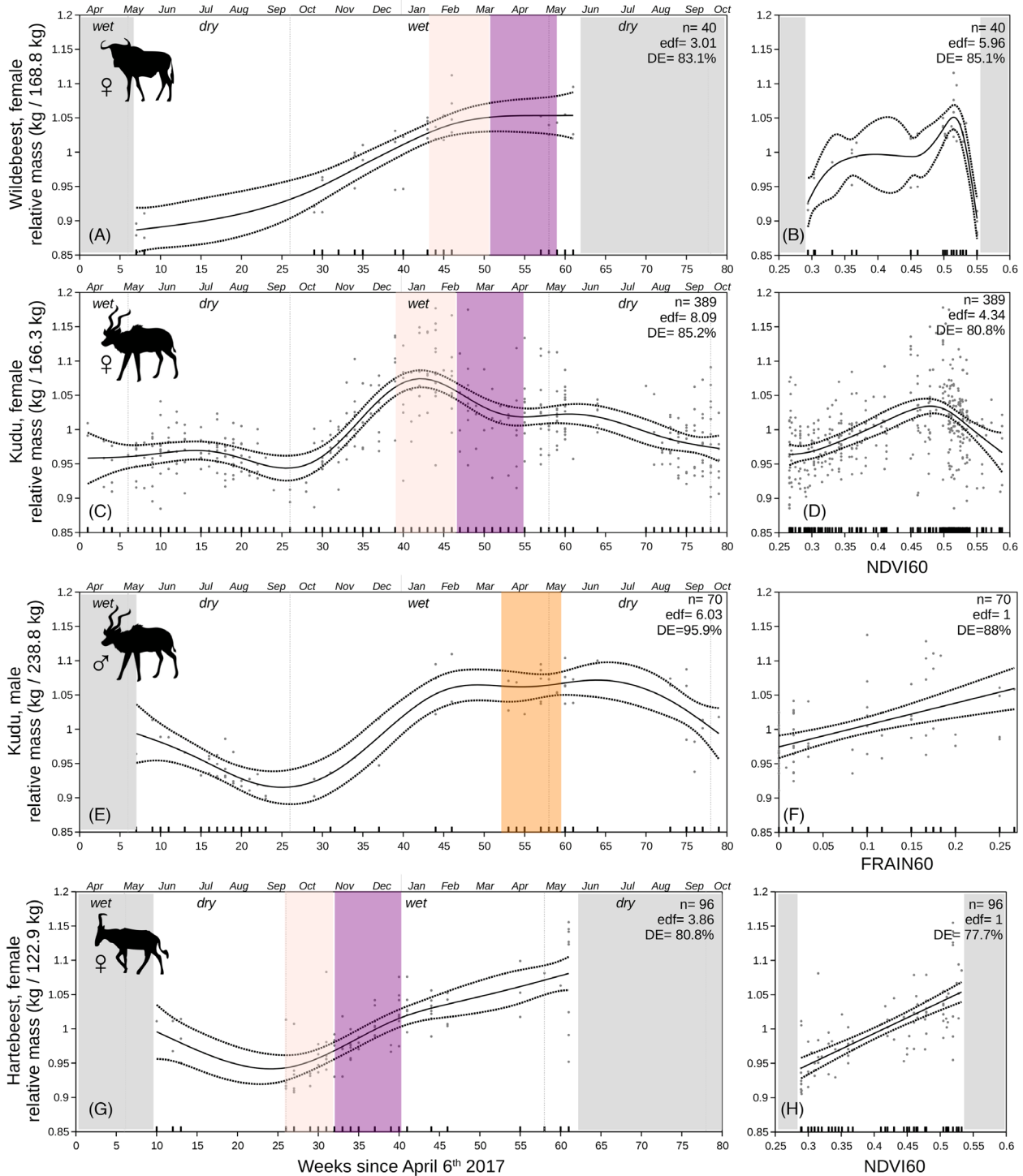


Figure 5. Modelled fluctuations of relative body mass over the study period, where (A and B) shows fitted curves for female blue wildebeest, (C and D) female greater kudu, (E and F) male greater kudu, and (G and H) female red hartebeest. Plots (A), (C), (E) and (G) show predictions for temporal trends, plots (B), (D) and (H) predictions for NDVI60, and plot (F) FRAIN60. “edf” refers to Effective Degrees of Freedom, and “DE” refers to Deviance Explained. Black continuous lines indicate fitted curves, black dotted lines are standard errors, grey dots are Pearson residuals, black marks at x axis indicate the x-location of residuals, and vertical grey lines represent starts/ends of wet and dry seasons. Grey areas visualize weeks beyond the first and last records for each group. Peach areas visualize when calving peaks typically occurs for each species (Estes, 1976; Nowak, 1997; Perrin, 1999; Spinage, 1973), purple areas visualize when heavy lactation period typically occurs for each species (Ayotte et al., 2019), and orange area in male greater kudu plot visualizes when the peak of mating season may be occurring (Castelló et al., 2016).

Bianchet, 2006), mountain goat (Mainguy & Côté, 2008) and Alpine ibex (Brivio et al., 2014)], which may be consistent with observations recorded here.

For male kudu, the recorded timing and duration of wet-season weight stabilization matched with the time when mating season occurred in the study area for this species (within 3 months after calving season, from week 52 to week 59; Estes, 1976; Owen-Smith, 1993; Perrin, 1999; Spinage, 1973). Therefore, potential for mass gain may have been tempered by the energy costs of competing for access to females (Mason et al., 2012). Female hartebeest was the only group that continuously gained mass during the wet season. In South Africa, this species gives birth at the beginning of the wet season (October–November; Nowak, 1997; Spinage, 1973), when body mass has additionally been impacted by resource scarcity from the previous dry season. Despite the confounding negative effect of reproduction and resource scarcity on body mass, mass gains during the first part of the wet season is likely to be constrained by energy expenditure for maternal care.

Availability of resources

Summed NDVI and the frequency of precipitation prior to a weighing event were both positively related to increased body mass of the study species in our savanna system. Elsewhere, NDVI was reported to have a positive effect on the condition of red deer in the Iberian Peninsula (Santos et al., 2018) assessed by measuring their kidney fat index (Riney, 1955). Similarly, the mass of hunted calves and yearlings of moose in Norway also related to NDVI (Herfindal et al., 2014). Rainfall has been positively related to the survival and reproduction of ungulates in Kenya (Ogutu et al., 2013) and, in central Italy, to the survival of Apennine chamois *Rupicapra pyrenaica* (Ferretti et al., 2019). In seasonal environments, reproduction often occurs only when NDVI is high (Côté & Festa-Bianchet, 2001; Paoli et al., 2018), suggesting that abundant resources facilitate nutritional condition suitable for breeding and investing in maternal care (Berkeley & Linklater, 2010; Cucco & Bowman, 2018; Ogutu et al., 2013, 2015; Peláez et al., 2017; Wittemyer et al., 2007).

Recent changes in seasonality, attributed to anthropogenic climate change, have included declining precipitation events and extended dry seasons. Such changes have been recorded in Southern Africa (decline in annual rainfall, Hodnebrog et al., 2016; Nhamo et al., 2019; Nhema-chena et al., 2020; projected increases in surface temperatures, Engelbrecht et al., 2015) and also more widely (Trenberth, 2011). Longer periods of water and nutritious vegetation scarcity may impact ungulate body condition to the point of affecting individual

survivorship. This may be especially true for grazers and mixed feeders that rely on seasonal vegetation pulses (Abraham et al., 2019), as well as for migratory ungulates that may have to travel longer distances looking for vegetation (Perkins, 2019). Beyond ungulates, Brawn et al. (2017) reported reduced survival of tropical birds that inhabit seasonal environments because of climate change, and Howard et al. (2018) predicted that pathways of migratory birds will become longer under future scenarios of climate change. Given the recent changes and projected future changes to climatic conditions, monitoring body mass changes could, and perhaps should, become a crucial monitoring tool to inform management. Short-term interventions could include supplying water, forage, vitamins and food supplements during unfavourable periods to minimize excessive mass losses; longer term, body condition monitoring could indicate which species may or may not thrive at a site. Such concerns could be particularly acute in regions such as South Africa when natural migratory pathways have been lost due to land-use development fragmenting natural landscapes. In addition, in many areas, wild populations are now effectively preserved in fenced reserves precluding natural movements away from unfavourable conditions.

The practicality of implementing remote mass monitoring in the African savanna

In this section, we describe some of the practical considerations of remote mass monitoring in savanna landscapes. The initial investment in equipment, whilst not cheap, is not punitively expensive and is likely to be within the budget of most sites that manage medium and large ungulates. Once the weighing station is deployed, its maintenance costs – visiting it fortnightly to check for damage and to change batteries and memory cards – are low. In our study, the initial investment was ~U\$1690 per weighing station, broken down as follows: (i) platform scale (range 0–3000 kg, accuracy ± 0.5 kg) with electric wires and reader cost U\$980 (LMI Ltd., Pretoria, South Africa), (ii) car battery cost U\$120, (iii) a salt block, which had to be replenished every 5–6 months, cost U\$25, (iv) camera trap cost U\$465, and (v) camera trap batteries and memory cards, plus ancillary equipment (hoses etc.) cost around U\$100. Iron rods and wire fences were recycled from elsewhere on site. During the 18 months of monitoring, only one station was damaged, when a mouse bit through the electric wires, and the problem was easily fixed. Moving weighing stations between sites requires suitable transport, as the scales can weigh up to 200 kg, and appropriate fencing must be deployed. Although white rhino were present at our site, and our system was sufficiently robust not to be damaged

by rhino, elephants (*Loxodonta africana*, the largest herbivore in the African savanna) were not present. Nevertheless, using a platform scale that can withstand their weight and replicating the fencing strategies that are used in areas with these animals should be enough to prevent damage. Theft of, for example, batteries and camera traps may need to be considered in more accessible areas. We deployed our weighing stations near permanent water bodies due to the attraction of mammals from across all areas to such sites, facilitating sampling of a wider breadth of individuals. Ecological characteristics of target species and the questions being addressed will help to inform the location and quantity of weighing stations. Home range extent could inform separation between scales when dealing with territorial species, and density of individuals may help to define the quantity of scales to deploy in a site. We suspect our study was affected by territoriality of males, because despite many adult females and juveniles of blue wildebeest and red hartebeest using the scales, only one adult male for each species was recorded during the 18 months of monitoring. Bait type could also be varied to target different species. We recorded two carnivores (white-tailed mongoose *Herpestes albicaudus*, black-backed jackal *Canis mesomelas*) and two primates (chacma baboon *Papio ursinus*, vervet monkey *Chlorocebus pygerythrus*) using the scale, but it seemed they were not attracted by the salt block. The biggest challenge and most time-consuming activity in our study was assigning a reliable ID to wild animals that have no tags or overt differentiating traits. Clearly, for studies on tagged individuals, or studies where population or cohort-level mean effects (*i.e.*, monitoring mass for individual age or sex classes, without need to identify individuals) are of interest, the latter challenge is greatly simplified.

Conclusions

We showed that it is possible to monitor and model seasonal variations of body mass in wild African ungulates on a near-daily basis, either at a population level or, when marked animals can be identified, on an individual basis. Our data come from only a small number of individuals of three species, inhabiting an intensively managed protected area. As such, they are unlikely to represent general trends in savanna ungulates. Nonetheless, the method we develop here provides an easy means to monitor body mass changes in a diverse range of wild ungulates, providing information which could be used in a variety of ways to enhance ecological understanding of systems. At a broad scale, more site-specific measures of body mass from across species' ranges can aid with understanding the drivers of spatial and temporal variation in body

mass. The method also has potential as an early-warning indicator by site managers, because changes across multiple measures of body mass might precede, and be easier to detect than, changes in the size of the population to which those individuals belong; thus, detecting changing body condition may enable managers to alter management to aid survival (Douhard et al., 2019) or reproduction (Lombardini et al., 2017; Newbolt et al., 2017; Podofillini et al., 2019) of target species. Monitoring body mass variations may be critical for protecting large herbivores that inhabit seasonal environments (Abraham et al., 2019; van der Merwe & Marshal, 2014; Wato et al., 2016), especially considering future climate change projections for savanna ecosystems, where precipitation events are typically expected to be reduced in frequency and volume (Trenberth, 2011).

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Total large herbivores hunted and captured to sell during study period (2016–2018). “M” refers to male, “F” to female, “T” to total hunted and captured. Indeterminate individuals are not reported and correspond to the difference between total individuals and sexed individuals.

Table S2. Description of models selected for female blue wildebeest. “edf” is effective degrees of freedom, “Ref.df” is reference degrees of freedom, “ML” is marginal likelihood, “Scale est.” is estimated scale parameter, “n” is sample size, and “ind” is number of different individuals.

Table S3. Description of models selected for female greater kudu. “edf” is effective degrees of freedom, “Ref.df” is reference degrees of freedom, “ML” is marginal likelihood, “Scale est.” is estimated scale parameter, “n” is sample size, and “ind” is number of different individuals.

Table S4. Description of models selected for male greater kudu. “edf” is effective degrees of freedom, “Ref.df” is reference degrees of freedom, “ML” is marginal likelihood, “Scale est.” is estimated scale parameter, “n” is sample size, and “ind” is number of different individuals.

Table S5. Description of models selected for female red hartebeest. “edf” is effective degrees of freedom, “Ref.df” is reference degrees of freedom, “ML” is marginal likelihood, “Scale est.” is estimated scale parameter, “n” is sample size, and “ind” is number of different individuals.