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Water provision alters wildebeest adaptive habitat selection and resilience in the Central Kalahari

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Abstract

Wildlife populations in semi-arid regions require unrestricted mobility along ecological gradients and across large landscapes to enable adaptive responses to seasonal variability and patchy resources. In the Kalahari region of Botswana, herbivore populations historically depended on seasonal access to the nutrient-rich Schwelle area in the wet season and to water from the Boteti River during drought periods. Blue wildebeest *Connochaetes taurinus* in the Central Kalahari Game Reserve (CKGR) have lost access to these key habitats due to fences and encroachment of livestock and humans. We deployed satellite collars onto 10 female wildebeest in the CKGR to examine seasonal movements and habitat selection in relation to the environmental conditions and fragmented ecosystem. Wildebeest favoured open, short-grass pan habitats in all seasons, probably in response to better forage quality and lower predation risk. The ability to remain in pan habitats during the dry season was a result of artificial water provision. A wildebeest herd that had no artificial water in its home range survived the dry season, whereas those wildebeest that were accustomed to water provision died when their water points failed in the dry season. Thus, water provision altered adaptive behaviour and reduced resilience of the population to the arid environment.

Résumé

Les populations sauvages des régions semi-arides exigent une mobilité sans restriction le long de gradients écologiques et au travers de vastes paysages pour pouvoir répondre de façon adaptative à la variabilité saisonnière et à la dispersion des ressources. Au Botswana, dans la région du Kalahari, les populations d'herbivores dépendent depuis toujours de l'accès saisonnier à la zone riche en nutriments en saison des pluies et à l'eau de la rivière Boteti pendant les périodes de sécheresse. Les gnous bleus *Connochaetes taurinus* de la Central Kalahari Game Reserve (CKGR) ont perdu l'accès à ces habitats essentiels à cause de clôtures et de l'envahissement du bétail et des hommes. Nous avons placé des colliers satellite sur dix gnous femelles de la CKGR pour examiner leurs déplacements saisonniers et la sélection des habitats en fonction des conditions environnementales et de la fragmentation de l'habitat. En toute saison, les gnous privilégiaient les habitats plats (*pan*), ouverts, couverts d'herbe courte, probablement pour la qualité de la nourriture et pour le plus faible risque de prédation. La possibilité de rester dans ces habitats plats en saison sèche était le résultat d'un apport d'eau artificiel. Un troupeau de gnous qui ne disposait pas d'eau « artificielle » dans son

territoire a survécu à la saison sèche alors que ceux qui étaient habitués à l'apport d'eau sont morts lorsque leurs points d'eau se sont taris en saison sèche. L'apport d'eau a donc modifié l'adaptabilité de leur comportement et réduit la résilience de la population face à un environnement aride.

1 | INTRODUCTION

Habitat loss and fragmentation compromise the resilience of wildlife populations to variable climatic conditions in semi-arid regions by restricting their mobility in response to stochastic patchy resources and habitat heterogeneity (Fryxell et al., 2005; Illius & O'Connor, 2000; Owen-Smith, 2004). In the 1970s, the Kalahari region of Botswana was home to some of Africa's most abundant herds of ungulates, with an estimated 250,000 blue wildebeest *Connochaetes taurinus* a similar number of red hartebeest *Alcelaphus buselaphus* and an estimated 100,000 springbok *Antidorcas marsupialis* (DHV, 1980). Owing to the low, patchy and unpredictable rainfall distribution of the region, these herds were extremely mobile, following a nomadic strategy in response to the rainfall-driven spatiotemporal mosaic of grazing resources in the landscape (Verlinden & Masogo, 1997; Williamson, Williamson, & Ngwamotsoko, 1988). The main wet season range of the blue wildebeest, hartebeest and springbok populations in the Kalahari ecosystem was a region with a high density of saline pans (Lancaster, 1978) between the Central Kalahari Game Reserve (CKGR) and the Kgalagadi Transfrontier Park (KTP), commonly known as the Kalahari Schwelle. The saline pans of the Schwelle probably enabled pregnant and lactating females to meet their elevated mineral requirements through access to mineral-rich forage and geophagy (Ayotte, Parker, & Gillingham, 2008; Williamson et al., 1988).

During dry seasons and mainly drought years, wildebeest made long distance movements from the Schwelle through the CKGR to the permanent water of the Boteti River, Lake Ngami and Lake Xau (450 km) and some to the south-west towards the Nossob River (150 km; Verlinden, 1998; Williamson et al., 1988). Fences in the north, east and south of the CKGR, as well as human and livestock encroachment in the Schwelle (Bergstrom & Skarpe, 1999; Cooke, 1985; Williamson et al., 1988) have increasingly restricted access to these various ancestral ranges. Furthermore, a recent review of national land use designated some of the Schwelle area (a part of a semi-protected wildlife management area) to the west of the CKGR as livestock ranches (Department of Lands 2009). This change will potentially exacerbate the isolation of the CKGR wildebeest population from the rest of the Kalahari population in the KTP and the Schwelle. These effects of habitat loss and fragmentation, and landscape change are believed to be responsible for the decline of the Kalahari ungulate populations, especially wildebeest, over the last 30 years (Wallgren et al., 2009), potentially through denied access to water, high-quality forage (Fryxell, Greever, & Sinclair, 1988; Oliver, Brereton, & Roy, 2013; Sinclair & Fryxell, 1985) and compromised persistence of plant–herbivore interactions (Fryxell & Sinclair, 1988). Wildebeest are the most water-dependent ungulates in the Kalahari and so loss of access to water in drought years results in mass die-offs (Williamson et al., 1988). Up to 80,000 wildebeest mortalities were cited in each drought year of 1961, 1964 and 1970 (Owens & Owens, 1984) and more than 50,000 were recorded in 1987 (Owens & Owens, 1984; Williamson et al., 1988).

The government of Botswana addressed the loss of access to drought ranges by establishing artificial waterholes in the CKGR in 1984 (Bonifica, 1992). Artificial water provision could remove the need to seek water, thereby selecting for a sedentary population, which may then decline due to local depletion of forage resources and ambush by carnivores around waterholes (Rosenstock, Warren, & James, 1999; Shannon, Matthews, Page, Parker, & Smith, 2009). It is unknown how the population that is potentially restricted within the CKGR is utilizing the landscape/habitat heterogeneity and its spatiotemporal variability within the reserve.

We studied habitat selection and movement patterns of the CKGR blue wildebeest population in response to seasonal resource variability. Pans and valleys usually have short, highly nutritious grasses compared to off-pan habitat (Milton, Dean, & Marincowitz, 1992); therefore, we expected that pan-valley habitat would have higher forage quality than off-pan habitat. However, in low rainfall areas, the herbaceous layer in the pans and valleys becomes moisture-limited earlier in the dry season than that in the sandy off-pan habitats, mainly because larger pore spaces in sands result in loss of hydraulic conductivity and conservation of soil moisture much later into the dry season than in clay soils (Alizai & Hulbert, 1970; Noy-Meir, 1973). This suggests that the off-pan habitat could provide greener forage during the dry season. We also expected a decline in forage abundance in the pan-valleys due to limited moisture and grazing. We predicted that wildebeest would select pan-valley habitat in the wet season. The forage maturation hypothesis proposes that herbivores aggregate to keep forage biomass at immature growth stages that are more nutritious than the mature forage (Fryxell, 1991; Wilmshurst, Fryxell, & Bergman, 2000). We expected wildebeest to remain in the pan-valleys during the wet season and maintain grazing lawns that provide high-quality forage and optimal levels of herbaceous biomass (Arsenault & Owen-Smith, 2008; Bonnet, Fritz, Gignoux, & Meuret, 2010). We also predicted that wildebeest would select the off-pan habitats during the dry seasons

where forage is expected to be greener than in the pan-valley habitat.

Predation risk avoidance may dominate the hierarchy of decision-making in habitat selection choices (Rettie & Messier, 2000). Thus wildebeest would be expected to select pan-valley habitats with their open short grassland, not only for the better forage quality of the pans but also for the lower predation risk that pans provide (Martin, Benhamou, Yoganand, & Owen-Smith, 2015). Artificial waterholes are also located in the pan-valley habitat, so in the dry season, wildebeest may be forced to use the pan-valley habitat to drink and sleep, even if they forage in the off-pan habitat, thereby extending their foraging area in the dry season. We therefore further predicted that wildebeest would cover shorter daily distances during the wet than dry seasons.

2 | MATERIALS AND METHODS

2.1 | Study area

The CKGR northern, eastern and western boundaries and Khutse Game Reserve (KGR) defined the extent of the study area at 21°00′–23°00′S and 22°47′–25°25′E (Figure 1a). The northern and eastern boundaries of the CKGR, as well as the eastern and southern boundaries of the KGR are fenced. The CKGR and the KGR cover 52,145 km² and 2,550 km², respectively. The area is hot and dry, with extreme temperatures ranging from −6°C to 43°C in winter and summer, respectively (DHV, 1980; Williamson & Williamson, 1985). Mean annual rainfall ranges from 350 to 400 mm (DHV, 1980). Although there is no permanent natural surface water in the reserves, water is provided for wildlife at 13 solar panel powered artificial waterholes. The area is dominated by Kalahari sandy arenosols with a wide distribution of pans and valleys on the Karoo basalt rock (DHV, 1980).

The CKGR and KGR contain five main habitats: pan and valley short grassland habitats, which are open and largely treeless with similar grass composition, and dune, interdunal and plains habitats, which are composed of savannah and woodland. For the purpose of this study, pans and valleys were classified as pan-valley habitat, and dunes, interdunal and plains as off-pan habitat because they generally have similar grass species. The herbaceous layer in the pan-valley habitat is dominated by _Leucosphaera bainesii_, _Eriocephalus_ sp., _Sporobolus ioclados_, _Enneapogon desvauxii_ and _Cenchrus ciliaris_, whereas the off-pan habitat is dominated by _Anthephora pubescens_, _Schmidtia pappophoroides_, _Stipagrostis uniplumis_ and _Urochloa trichopus_. The pan-valley habitat contains islands of _Acacia sp._ and _Boscia albitrunca_, and the off-pan habitat is dominated by _Rhigozum trichotomum_, _Catophractes alexandrii_, _Grewia sp._, _Acacia sp._, _Albizia anthelmintica_, _Lonchocarpus nelsii_, _Terminalia sericea_ and _B. albitrunca_ (Bekker & De Wit, 1991). Nomenclature for all plant names is according to Germishuizen, Meyer, Steenkamp, and Keith (2006). The faunal composition includes ungulates such as giraffe _Giraffa camelopardalis_, eland _Taurotragus oryx_, blue wildebeest, gemsbok _Oryx gazella_, kudu _Tragelaphus strepsiceros_ and springbok. Carnivores are also present, such as lion _Panthera leo_, leopard _Panthera pardus_, cheetah _Acinonyx jubatus_, wild dog _Lycaon pictus_, spotted hyaena _Crocuta crocuta_, brown hyaena _Hyaena brunnea_ and black-backed jackal _Canis mesomelas_. Nomenclature for the animals is according to Skinner and Chimimba (2005).

2.2 | Collaring and movement dataset

We fitted GPS Plus satellite collars manufactured and programmed by Vectronic Aerospace GmbH (Vectronic Aerospace, Berlin, Germany) to 10 female wildebeest in different herds each ranging in size from 6 to 33 individuals, between August 2011 and July 2014. Four collars were deployed in August 2011, one each in May 2012, July 2012 and September 2012 and three in November and December 2012. All 10 herds were located the pan-valley habitat when they were darted. One of three experienced wildlife veterinarians registered with the government of Botswana carried out each darting and collaring operation, as approved by the Ministry of Wildlife Environment and Tourism through a research permit, capture and darting permits. All darted animals were adult females in good condition that were not obviously pregnant or with a young calf. Every effort was made to minimize the stress to darted wildebeest and their herds. All the animals were darted from a vehicle and we avoided darting

FIGURE 1 Map (a) of the study area showing both CKGR (Central Kalahari) and Khutse Game Reserve (Khutse), vegetation sampling, waterholes and collaring sites. Map (b) movement locations of a migratory herd between 2012 and 2014. The wet season range was in the northern CKGR (November to March), whereas the dry season range was at southern CKGR, KGR and south-west of KGR (April to October)
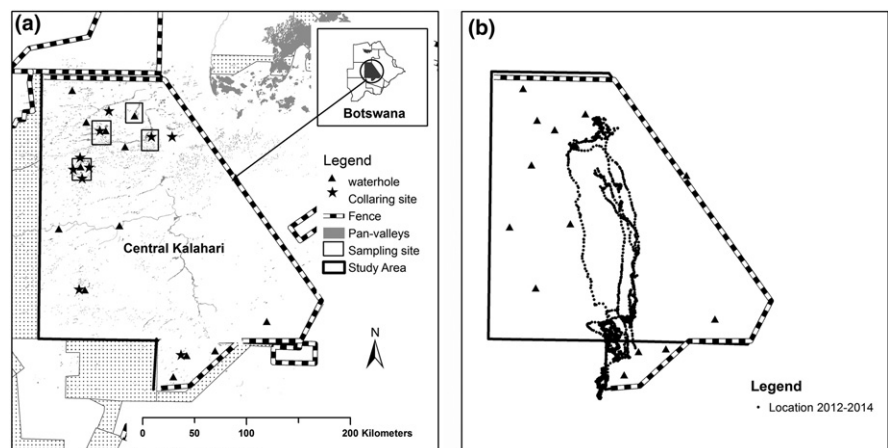
during the hottest time of day. We drove approached herds until animals were comfortable around with our vehicle before darting, which took between 10 min and 2 hr depending on the responses of the herds. The wildebeest were immobilized with 5 mg of Etorphine and 100 mg Azaperone, and the tranquilizer was reversed with 25 mg of Diprenorphine. The Etorphine and Diprenorphine were manufactured by Novartic, Switzerland and Azaperone by Kyron laboratories, South Africa. Reusable Palmer Cap-Chur aluminium dart syringes with barbed needles were used with a Pneu-dart Model 389 remote delivery system. The animals were monitored after drug reversal, and we left as soon as they re-joined and were accepted by the herd. All the satellite collars were removed from the animals after the study, including three that had stopped transmitting prematurely.

Collars were programmed to record hourly Geographical Positioning System (GPS) fixes. We screened all the recorded GPS locations and removed locations with a high dilution of precision (DOP > 9) and a low number of satellites (<3D; D'Eon & Delparte, 2005; Frair et al., 2010; Lewis, Rachlow, Garton, & Vierling, 2007). We converted all data from decimal degrees to a UTM coordinate system to allow distance and area estimations. We determined location error of the satellite collars by calculating the distance between the true location of the collar and the collar GPS locations from a stationary collar (Lewis et al., 2007). The location error (mean $\pm$ *SE*) was 6.8 $\pm$ 4.9 m. High mortality of study animals (associated with water availability as discussed later in the results), combined with the overall small size of the study population, led to fewer than five datasets during any one season; we therefore used cumulative seasonal data from 2011 to 2014.

2.3 | Seasonal analysis

We divided each year into wet, early dry and late dry seasons, based on average rainfall and temperature patterns for the area, which influence surface water availability and forage conditions. Wet and late dry seasons are usually very hot (up to 43°C) while early dry season is very cold (−6°C). Due to high variability of the onset date of the three seasons, we focused our analysis on two peak seasonal months to create a clear distinction between seasons. We used January and February for the wet, June and July for the early dry, and September and October for the late dry seasons, respectively.

2.4 | Forage quality and quantity between habitats

During each season, we randomly sampled vegetation in five 0.5 × 0.5 m quadrats from 11 sites in each of the two habitat types: pan-valley and off-pan. The pan-valley sites were in northern pan-valley system, and the off-pan sites were around these pan-valley sites (Figure 1a). At each site, the first quadrat was thrown randomly to provide a starting point and the other four quadrats were systematically located 5 m from the first quadrat in the four cardinal directions. We recorded the height (to the tip of inflorescence or culm) of five grasses in each quadrat, selected at random. Grass samples were

clipped to 1 cm above ground from all quadrats. Due to extremely low amounts of grass in some seasons and habitats, grass samples from the quadrats were combined for each site. We air-dried the samples in the field and further dried them in an oven at 60°C for 48 hr. Dry biomass was used as a measure of forage quantity. We ground each sample and mixed it well to get a homogeneous representative subsample and analysed it for crude protein (nitrogen %), with a LECO nitrogen analyser at the Biological Sciences Department, University of Botswana. We then analysed subsamples for mineral content (phosphorus, sodium and calcium), using ICP-AES spectrometry at the Okavango Research Institute, University of Botswana.

We used generalized linear mixed models (lme4 package; Bates, Maechler, Bolker, & Walker, 2015), in R version 3.2.4 to compare grass quality (protein, calcium, sodium and phosphorus) and quantity (biomass and height) between habitats and seasons. Response values were all positive but did not follow a normal distribution, so we used a gamma distribution. Habitat, season and the interaction between the two were used as fixed effects and replica within site was used as a nested random effect.

2.5 | Habitat selection

Shapefiles of pans and valleys were obtained from the Department of Survey and Mapping and used to develop a habitat map at a scale of 1:3,600,000. We used the "Minimum Bounding Geometry" tool in ArcGIS 10.3 to calculate 100% Minimum Convex Polygons (MCP) from seasonal movement data to determine the potential area available to each animal. We used the movement-based kernel density estimation (MKDE) method from the adehabitatHR package in R (R Development Core Team, 2015) to calculate the seasonal utilization distribution (UD) and home range (HR) for each individual (Benhamou, 2011). We set the minimum distance threshold (MDT) to 10 m, the distance below which the animal was considered to have been inactive or resting and set the minimum smoothing parameter to 30 m. We used UD-weighted grids within the HRs to estimate pan-valley and off-pan use and availability to determine third order habitat selection patterns (Johnson, 1980). We used Jacobs' index to calculate habitat selection ratios (Jacobs, 1974; Kauhala & Auttila, 2010)

$$D = \frac{r - p}{r + p - 2rp}$$

where *r* is the proportion of habitat used and *p* the proportion of habitat available. *D* varies from −1 (avoidance) to +1 (preference), and values close to zero indicate that the habitat is used in proportion to its availability. We used multivariate analysis of variance (MANOVA) in R version 3.2.4 to determine whether selection ratios differed between seasons.

2.6 | Daily distance analysis

We used hourly location data from collared wildebeest to calculate the minimum daily distance covered. We adopted the method of

distance calculation from Ensing et al. (2014), as modified in http://www.movable-type.co.uk/scripts/latlong.html, to calculate hourly distance, and summed the hourly distances for each day and for each animal. We used generalized linear mixed models (Bates et al., 2015) to compare the daily distance covered between seasons, with the fixed effect of year to account for annual differences and the random effect of individual. During the study, four artificial waterholes used by study animals dried up due to borehole breakdown and there was some observed change in the foraging behaviour of the animals. We compared our results with and without the affected collared animals. We also demonstrated the effects of changing water availability, by comparing wildebeest movement a month before and after the waterhole dried up. The generalized linear mixed models (lme4 package; Bates et al., 2015), in R version 3.2.4, were used to compare pre- and postperiod waterhole drying periods. Response values were all positive but did not follow a normal distribution, so we used a gamma distribution. All statistical analyses were done in R 3.2.4 (R core team, 2015).

2.7 | Model selection

We ran all possible combinations of models for the above variables (except for habitat selection analysis) and identified the most parsimonious based on Akaike's information criterion (AIC; Akaike, 1974). We considered models to be competitive if their AIC values were within two units of the best model, and slightly competitive if there were between 3 and 7 (Burnham & Anderson, 2002).

3 | RESULTS

3.1 | Forage quality

Our results confirmed that forage quality in terms of protein, phosphorus and calcium, in the pan-valley habitat was higher than in the off-pan habitat, except during the late dry season. The full models, with or without an interaction term, provided the best fit for protein, calcium and phosphorus (Table 1). Protein content decreased from the wet season to the early dry and late dry seasons in the pan-valley habitat, but the decrease in the off-pan habitat was small between the dry seasons (Figure 2a). In the pan-valley habitat, calcium decreased from the wet season to the early dry and late dry seasons, but did not change between the early dry and the late dry seasons in the off-pan habitat (Figure 2b). Phosphorus was higher in the wet than the early dry and the late dry seasons. Phosphorus was higher in the in the pan-valley than off-pan habitat (Figure 2c). For sodium, the most parsimonious model included both fixed effects of season and habitat. Sodium was higher in the wet than the early dry season and the late dry season (Figure 2d).

For grass biomass, the model with the best fit was the global model, which included the fixed effects of season and habitat, and the interaction between the two terms. Biomass was lower in the pan-valley habitat than in the off-pan habitat, but within the off-pan habitat, there was no seasonal difference. In the pan-valley habitat,

there was a difference between the wet and early dry seasons but not between the early dry and late dry seasons (Figure 3a). For grass height, the model with the best fit was the global model, which included the fixed effects of season and habitat, and the interaction between the two terms. Grass height was lower in the pan-valley than in the off-pan; it decreased from the wet season to the early dry season in the pan-valley habitat, but increased from wet to early dry in the off-pan habitat (Figure 3b). Therefore, sandy off-pan habitats had higher grass biomass and height than pan-valley habitats throughout the year.

3.2 | Wildebeest habitat selection

Wildebeest strongly selected for the pan-valley habitat in the CKGR, with a mean ($\pm SE$) Jacob's index of 0.64 ± 0.065, 0.68 ± 0.10 and 0.60 ± 0.10 in the wet, early dry and late dry seasons, respectively. However, habitat selection did not change significantly between

TABLE 1 Ranking of possible models for forage quality and quantity

Model variables	Δ_{AIC}	ω	k	Deviance
Protein				
Habitat × Season	0	0.737	3	2.009
Habitat + Season	2.203	0.245	3	2.258
Null	45.239	0.000	2	4.521
Calcium				
Habitat × Season	0	0.706	3	9.460
Habitat + Season	3.377	0.130	3	10.601
Season	2.919	0.164	2	10.547
Null	28.066	0.000	2	16.294
Phosphorus				
Habitat + Season	0	0.4724	3	18.759
Habitat × Season	1.638	0.2083	3	20.425
Season	0.7838	0.3193	2	20.756
Sodium				
Habitat + Season	0	0.452	3	28.843
Habitat × Season	1.118	0.258	3	30.095
Season	0.884	0.290	2	31.167
Null	46.171	0.000	2	63.344
Height				
Habitat × Season	0	1	3	509.977
Null	102.967	0.000	2	563.469
Biomass				
Habitat × Season	0	0.984	3	103.718
Null	23.159	<0.001	2	154.405

Delta (Δ) AIC = difference between model AIC and lowest AIC in the model set. ω = Akaike model weight, "weight of evidence" in favour of model, adding to 1. k = number of estimable parameters in the model. Deviance = measure of model fit. The model covariates include habitat and season. Only models with Δ_{AIC} values less than four units and the null model are presented.
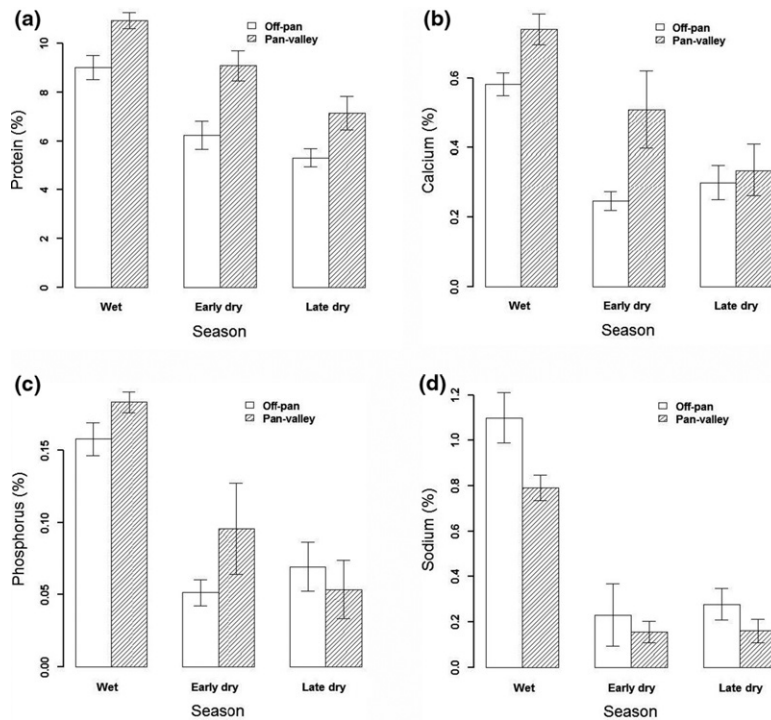
FIGURE 2 Seasonal mean dry mass percentage ($\pm SE$) for grass crude protein (a), calcium (b), phosphorus (c) and sodium (d) between pan-valley and off-pan habitats in the CKGR and KGR
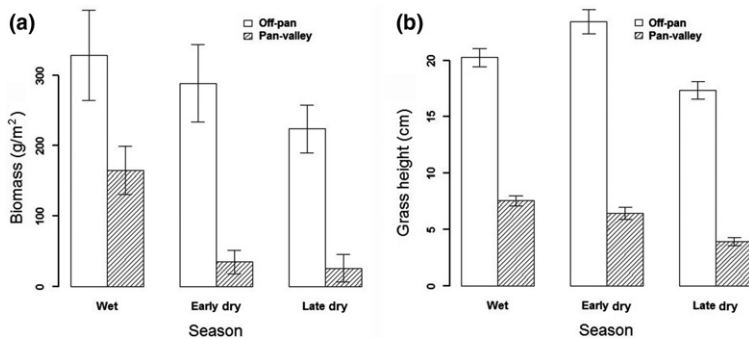

FIGURE 3 Seasonal mean ($\pm SE$) values for grass dry biomass (a) and height (b) in between pan-valley and off-pan habitats in the CKGR and KGR

seasons (Table 2). Although most herds selected the pan-valley habitat throughout the year, one was migratory, occupying distinct seasonal home ranges: wet, early dry and late season ranges in the northern CKGR, the southern CKGR and KGR and outside the western KGR, respectively (Figure 1b). There was a distance of over 200 km between the wet and dry season home ranges.

3.3 | Daily distance

One wildebeest covered extreme daily distances at an average of 40.56 ± 15.64 km/day during the late dry season of 2011, with a longest minimum daily distance of 84.48 km. Data from this animal were not included in the analysis for the population because it was a substantial outlier. Wildebeest covered mean ± SE daily distances of 6.89 ± 0.15 km, 7.59 ± 0.28 and 6.71 ± 0.17 km during the wet, early dry and late dry seasons, respectively. The most parsimonious model included the effect of year and season; the null model was not competitive (Δ_{AIC} = 0, ω = 1, k = 8, Deviance = 346.2347). Wet and early dry season distances were not different, whereas the

TABLE 2 MANOVA results for seasonal comparison of habitat selection ratios. No significant results found

Season	Habitat	MANOVA output
Wet vs. Early Dry	Overall	Pillai$_{2,14}$ = 0.0983, p = .510
	Pan-valley	$F_{1,14}$ = 0.848, p = .775
	Off-pan	$F_{1,14}$ = 0.102, p = .754
Wet vs. Late Dry	Overall	Pillai$_{2,15}$ = 0.237, p = .131
	Pan-valley	$F_{1,15}$ = 0.124, p = .730
	Off-pan	$F_{1,15}$ = 1.401, p = .254
Early vs. Late Dry	Overall	Pillai$_{2,11}$ = 0.0580, p = .720
	Pan-valley	$F_{1,11}$ = 0.252, p = .625
	Off-pan	$F_{1,11}$ = 0.558, p = .469

late dry season distance was shorter than in the early dry season. Daily distances in late dry season of year 2011, early dry season of 2012 and wet season of 2013 were longer than the other years, respectively. When data from wildebeest that were affected by waterholes drying up were included, mean daily distances increased,

and the wet season distance was not different from the late dry season, whereas the early dry distance was longer than the other seasons. Daily distances early dry season of 2012 and wet season of 2013 were longer than the other years, respectively.

For daily distances travelled before and after the waterholes dried up, the most parsimonious model included the effect of water availability; the null model was not competitive ($\Delta_{AIC} = 0$, $\omega = 1$, $k = 2$, deviance = 126.538). Distance travelled was shorter before (5.93 ± 0.97) than after (13.35 ± 0.25) the waterhole dried up. Seven (70%) of the 10 collared animals made long distance movements (up to 275 km) when the waterholes they depended upon dried up. Five (71%) of the seven collared wildebeest that left their range after a waterhole dried up died before finding an alternative waterhole. Lions killed three collared wildebeest inside the reserve, while two left and died outside the reserve, one from apparent dehydration and the other from unknown causes.

4 | DISCUSSION

Our results show that wildebeest strongly select for the pan-valley habitat in the CKGR throughout the year. Pans were favoured year-round because of their shorter grasses, and higher crude protein, calcium and phosphorus content. Unlike in other areas where forage quantity during the dry season influenced habitat selection of large herbivores (Anderson et al., 2005; Saïd et al., 2009), the decline in abundance and quality of forage from the wet to dry seasons did not influence wildebeest foraging patterns. Thus, they are not limited by forage quantity in this ecosystem. Wildebeest are adapted for foraging on relatively short-sward grasslands (Arsenault & Owen-Smith, 2008; Murray & Illius, 2000; Wilmshurst et al., 2000), which may explain why they did not select taller grass in the off-pan habitat, even during the dry season.

The key wet season range of wildebeest in the Serengeti is a vast treeless saline grassland, similar in grass composition and function to the smaller scale pans in the CKGR. Most pans in the CKGR are dominated by halophytic grasses such as *Sporobolus ioclados*, as are the short-grass saline plains of the Serengeti (McNaughton, 1983), suggesting functional similarities between these key wet season ranges. Habitats selected by wildebeest in the Kruger National Park (Grant & Scholes, 2006; Yoganand & Owen-Smith, 2014) and by some zebra in northern Botswana (Fynn, Chase, & Röder, 2014) show similar functional similarities, with relatively high protein and phosphorus content. A higher concentration of protein and minerals help to meet the elevated resource demands of pregnant and lactating females during the wet season (Kreulen, 1975; Murray, 1995; Voeten, van de Vijver, Olff, & van Langevelde, 2010) and build body stores from abundant forage to survive the dry seasons (Parker, Barboza, & Gillingham, 2009).

Habitat quality is likely to be a key determinant of habitat selection for Kalahari ungulates (e.g., Milton et al., 1992), but it is difficult to disentangle the relative influence of habitat quality and antipredator behaviour on selection for pan habitats (Fryxell, 1991; Yoganand

& Owen-Smith, 2014). The open high-visibility nature of the pans, greatly reduces predation risk (Hernández & Laundré, 2005; Valeix et al., 2009), but strongly co-varies with the higher forage quality of the pans. Therefore, predation risk could also contribute to selection for the pan-valley habitat, especially at night (Martin et al., 2015), when predators are most active (Hayward & Slotow, 2009). All the predation events on collared animals were in the off-pan habitat, emphasizing that pan-valleys provide a much safer habitat. Therefore, the extent and hierarchy of the influence of forage quality and predation risk factors cannot be easily defined and ranked. Thus, in the Kalahari and other savannah ecosystems, wildebeest take advantage of the low predation risk nature and higher forage quality of the pan habitats, thereby maintaining growth and reproductive processes and reducing predation events.

Our results also suggest that water is a critical component of wildebeest home ranges, especially when they become accustomed to artificial water provision (Owen-Smith, 1996; Western, 1975; Williamson et al., 1988), and therefore influences movement patterns across the landscape (Smit, Grant, & Devereux, 2007). During the wet season, the pan-valley habitat had above-optimal grass height and biomass for a grazer the size of a wildebeest (Wilmshurst et al., 2000), but wildebeest remained on the pans during the dry season when grass height and biomass had dropped to 25 g/m^2, well below optimal levels (94 g/m^2) for wildebeest (Wilmshurst et al., 2000). Provision of artificial water points in the pans seemed to have influenced the dry season movement patterns. One wildebeest herd at a pan without a water point migrated away during the dry season, and other wildebeest left pans when artificial water points failed during the dry season. This suggests that water availability during the dry season was a key limiting factor that influenced habitat selection.

The migratory herd moved over 200 km from its wet season range to the southern CKGR, apparently attracted to a high abundance of tsamma melons *Citrullus lanatus* and gemsbok cucumber *Acanthosicyos naudinianus* (M. Selebatso, pers. obs.) and to a burned area during the late dry season. The southern migration of this herd might be driven by a need for water provided by the tsamma melons and the likelihood of green regrowth following fires. Moisture provided by these melons could explain why this herd survived the entire dry season without access to a waterhole. Knight, Knight-Eloff, and Bornman (1987) suggested that wildebeest in the KTP depended on these water-bearing plants when they did not have access to water. In support of this, all the other herds that had access to artificial water were sedentary and did not leave the high-quality pan-valley habitat as long as water was available. This suggests that water provision has resulted in a loss of adaptive foraging knowledge in water-dependent individuals because all those that were unable to find alternative water points after the water point in their favoured pans dried up died, whereas the migratory herd survived both dry seasons without evidence of accessing a waterhole.

Contrary to our predictions, but consistent with findings by Hopcraft et al. (2014) in East Africa, wildebeest daily movement distances were smaller in the late dry season than in the other seasons, though not significantly different from the wet season. The late dry

season was when forage availability was lowest and temperatures were generally very high. Wildebeest probably attempted to conserve energy and avoid heat stress during the late dry season by minimizing their movements (Selebatso, Fynn, & Maude, 2017). The inconsistent availability of water seems to not only affect habitat selection, but also energy expenditure and risk, as the wildebeest had to extend their daily distances following the loss of water. The nonmigratory wildebeest made long distance movements after the artificial waterholes in their home ranges dried up. The drying up of artificial waterholes seemed to push wildebeest to take greater risks through increased exposure to predation and the potential to lose condition in an attempt to seek alternative sources of water. Collared wildebeest made exploratory searches for alternative water sources, and the majority died during the search. Our results emphasize the need for water provision, especially that removal of anthropogenic factors such as fences and land use changes are highly unlikely. The provision of artificial water for wildlife in arid environments disrupt natural processes (Andrew & Lange, 1986; Thrash, 1980; Grant et al., 2002), but when access to key resources are restricted, much of the natural ecosystems resilience is lost (Fahrig, 2007; Primack, 2002). Maintenance of water-dependent species in drylands may therefore depend on such artificial water provision, especially given the continued human-induced habitat fragmentation and connectivity loss. Furthermore, Owens and Owens (1984) reported high mortalities of wildebeest due to illegal hunting and range degradation by livestock in and around Lake Xau, where most of the wildebeest went in the last recorded drought migration. We therefore emphasize the need for timely maintenance of existing waterholes in the CKGR to reduce future mortalities that could result from the drying of the waterholes.

In conclusion, high-quality forage in pans and valleys, combined with access to water and reduced predation risk, are important determinants of the habitat selection and movement patterns of Kalahari wildebeest. Seasonal forage availability, temperature and water availability limited the movement patterns and home ranges. Artificial water provision in arid ecosystems is important to compensate for lost access to natural water sources; however, it promotes a sedentary strategy and loss of adaptive resilience to shocks, such as water points failing. Our results reveal how loss of connectivity and access to seasonal resources could lead to complex consequences for species reliant on access to distinct seasonal ranges and key resources. If artificial water development is a necessary option for wildlife management in arid environments, a clear maintenance programme is required to ensure consistency in the provision of water.

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