**ARTICLE**

# Factors influencing the diurnal behaviour of white rhino (*Ceratotherium simum*) in Matobo National Park, Zimbabwe

Tafadzwa Tichagwa[1,2] (iD) | Nicola Pegg[1] | Hilton G. T. Ndagurwa[2,3] (iD) | Colum Zhuwau[4]

[1]Dambari Wildlife Trust, Bulawayo, Zimbabwe

[2]Department of Forest Resources & Wildlife Management/Forest Ecology Laboratory, Faculty of Applied Science, National University of Science & Technology, Bulawayo, Zimbabwe

[3]School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Wits, South Africa

[4]Scientific Services, Matobo National Park, Parks and Wildlife Management Authority, Kezi, Zimbabwe

**Correspondence**
Tafadzwa Tichagwa, Dambari Wildlife Trust, P.O. Box 3863, Bulawayo, Zimbabwe.
Email: tichagwatafadzwa91@gmail.com

**Funding information**
Whitley Wildlife Conservation Trust; Marwell Wildlife

## Abstract

Activity periods and diurnal behaviour of southern white rhino (*Ceratotherium simum simum*) were studied in Matobo National Park, Zimbabwe, from August 2016 to July 2017 using camera trapping and focal group sampling, respectively. Camera trap data showed that diurnal and nocturnal movements of white rhino varied significantly with moon phase, with more frequent nocturnal photographic captures during full- and third-quarter moon phases than during new and crescent moon phases. Permutational MANOVA and canonical correspondence analysis of focal group observation data were used to test the effects of season, time of day, habitat type, distance to roads, moon phase, presence/absence of other mammals, age/sex category, individual identity and herd composition on daytime behaviour. Weather conditions accounted for the majority of variation in rhino behaviour, with more time spent feeding during cloudy and rainy weather than sunny weather. Time of day and moon phase also accounted for high variation in behaviour, followed by habitat attributes and age/sex category. Variance partitioning by sets of explanatory variables showed that weather conditions had the greatest explanatory power in the variation of rhino behaviour, followed by temporal attributes, habitat attributes and age/sex category. Our findings provide insights for white rhino population management strategies aimed at increasing the effectiveness of security patrols, minimising disturbance and improving sightings for tourists.

## Résumé

Les périodes d'activité et le comportement diurne du rhinocéros blanc du sud (Ceratotherium simum) ont été étudiés dans le parc national de Matobo, au Zimbabwe, d'août 2016 à juillet 2017 en utilisant respectivement des pièges photographiques et une méthode d'échantillonnage des groupes focaux. Les données des pièges photographiques ont montré que les mouvements diurnes et nocturnes du rhinocéros blanc variaient considérablement en fonction des phases lunaires, avec des captures photographiques nocturnes plus fréquentes pendant les phases de pleine et de trois quarts de lune que pendant les phases de nouvelle lune et de croissant de lune. Une MANOVA (analyse de variance multivariée) permutationnelle ainsi qu'une analyse de la correspondance canonique des données d'observation des groupes focaux ont été utilisées pour étudier l'impact des saisons, des heures de la journée, du type d'habitat,

de la distance aux routes, des phases lunaires, de la présence ou absence d'autres mammifères, de la catégorie d'âge ou de sexe, de l'identité individuelle et de la composition des troupeaux sur le comportement diurne. Les conditions météorologiques expliquent la majorité des variations du comportement des rhinocéros, qui passent plus de temps à se nourrir par temps nuageux et pluvieux que par temps ensoleillé. Les différentes heures de la journée et phases lunaires expliquent également une forte variation du comportement, suivies par les caractéristiques de l'habitat et la catégorie d'âge ou de sexe. Le fractionnement de la variance en ensembles de variables explicatives a montré que les conditions météorologiques constituaient la meilleure explication de la variation du comportement des rhinocéros, suivies par les caractéristiques temporelles, les caractéristiques de l'habitat et la catégorie d'âge ou de sexe. Nos résultats fournissent des informations sur les stratégies de gestion de la population des rhinocéros blancs visant à accroître l'efficacité des patrouilles de sécurité, à minimiser les perturbations et à améliorer les observations pour les touristes.

**KEYWORDS**
camera traps, diurnal behaviour, focal group sampling, Matobo National Park, Zimbabwe

## 1 | INTRODUCTION

The continual monitoring of protected areas is an essential component in the conservation of important species such as the white rhino (*Ceratotherium simum*, Burchell 1817; Hutchins & Kreger, 2006). Likewise, understanding behavioural patterns of this species in relation to prevailing climatic conditions, habitat attributes and sociality should also be considered vital when developing conservation strategies (Belovsky & Slade, 1986; Hutchins & Kreger, 2006; Jordaan, Brown, & Slater, 2015; Rachlow, 1997; Wardjomto, 2013). White rhino are continually in danger because of poaching and habitat loss (Hutchins & Kreger, 2006), and this species is listed as Near Threatened by the International Union for Conservation of Nature (IUCN; Emslie, 2012). However, despite the threats facing white rhino populations globally, studies on the diurnal behaviour of this species, particularly in Zimbabwe, are limited (Condy, 1973; Monks, 1995; Rachlow, 1997). Understanding behavioural patterns of white rhino populations in human-managed ecosystems is essential for establishing a population's social and energetic needs, its role in the trophic dynamics of the system (Belovsky & Slade, 1986) and effective security.

Very large herbivores, such as white rhino, are subject to physiological constraints that affect activity patterns. Large body size confers high energetic demands and necessitates a substantial time allocation to feeding, particularly in environments with forage resources that are patchily dispersed in space and time (du Toit & Yetman, 2005). Large mammals also have high thermal inertia, which affects the ability to dissipate heat, and may exhibit behavioural thermoregulation mechanisms, such as restricting active behaviours to cooler weather, selecting shaded habitats or wallowing (Owen-Smith, 1988). White rhino have been found to be active during the early and late periods of the day when it is cooler (Monks, 1995; Owen-Smith, 1973). Avoiding disturbance and the associated costs of vigilance may also be an important factor controlling habitat selection and activity patterns (Mohd-Azlan, Kaicheen, & Yoong, 2018).

The white rhino engages in behaviours such as feeding, walking, resting, wallowing and socialising (Condy, 1973; Hutchins & Kreger, 2006; Monks, 1995; O'Connor, 1986; Owen-Smith, 1973) that need to be timed in an ideal manner throughout the day to ensure adequate time allocation to each activity (Owen-Smith, 1988). Daily and seasonal organisation of behaviour is modified by both external factors—for example environmental conditions such as ambient temperature (Owen-Smith, 1988); changes in the light–dark cycle (Leuthold, 1977; Shi, Dunbar, Buckland, & Miller, 2003); and resource availability and disturbance (Hutchins & Kreger, 2006; Kiwia, 1989; Mehradadfar, 1999)—and internal factors such as physiological state and behavioural sequences (du Toit & Yetman, 2005; Leuthold & Leuthold, 1978; Leuthold, 1977; Owen-Smith, 1973; Shi et al., 2003). Time allocation to one behaviour by animals results in them losing opportunity to gain the benefits offered by other activities, thereby incurring energetic costs (Owen-Smith & Goodall, 2014; Shi et al., 2003). As has been found elsewhere, it is important to consider the interplay between environmental conditions, anthropogenic disturbances and physiological factors that shape the behavioural patterns of large mammals in order to formulate and execute effective conservation strategies (Notarbartolo-di-Sciara, Hanafy, Fouda, Afifi, & Costa, 2009).

Our study site, Hazelside section of Matobo National Park (MNP), is home to a free-ranging white rhino population that is thriving in a human-managed ecosystem characterised by activities such as nonconsumptive tourism, vehicular traffic and periodic permitted harvesting of nontimber forest products (NTFPs). Through the

use of camera traps, we investigated activity patterns of white rhino through day–night, moon phase and seasonal cycles. Detailed daytime observations were also conducted to test whether habitat attributes (habitat type and distance to roads as a proxy for disturbance), prevailing climatic conditions (season and weather conditions), temporal attributes (moon phase and time of day) and sociality (white rhino age/sex category, social grouping and presence/absence of other mammals) influenced the diurnal behaviour patterns of white rhino. Apart from being large-bodied, white rhino also have relatively poor eyesight although they navigate by sight (Owen-Smith, 1973). Key assumptions were that white rhino would express behaviours and habitat selection to maximise forage intake, avoid thermal stress and minimise energy expenditure, for example through avoiding disturbance and reducing vigilance.

## 2 | MATERIALS AND METHODS

### 2.1 | Study site

The study was conducted in south-western Zimbabwe in a 72-km$^2$ area within the northern (Hazelside) section of MNP (located between 20°30′ and 28°33′) and the adjacent Rhodes Matopos Estate (located between 20°22′ and 28°32′). The area is semi-arid lying within agro-ecological zone IV of Zimbabwe (Kumirai, Msimanga, Munyikwa, Chidavaenzi, & Muringaniza, 2003). Mean annual rainfall is 623 ± 45 SE mm (Gordon Park Boy Scouts Camp unpubl. data), received mainly between mid-November and March though the timing and occurrence are erratic (Lunt, 2011). Water is available perennially from two small dams in the north, from pools along rivers and from natural springs (Figure 1). Supplementary feed is not provided, but human harvesting of grass resources in the cool dry season, particularly in the central and southern zones of the study area, provides swards of preferred height from July. Daytime maximum temperatures average 32.8°C, while average night temperatures can drop below 10°C, and frost is not uncommon in the cool dry season (Kumirai et al., 2003). October is the hottest and July the coolest month. There are three distinct seasons, which are the hot dry (September–November), hot wet (mid-November–April) and cool dry (May–August).

The vegetation of the study area is diverse due to the assortment of granite landforms and variable exposure to moist south-easterly airflow during the dry season (Kumirai et al., 2003). Accumulations of nutrients and moisture at the base of rocky outcrops give rise to dense woodland dominated by species such as *Pterocarpus*
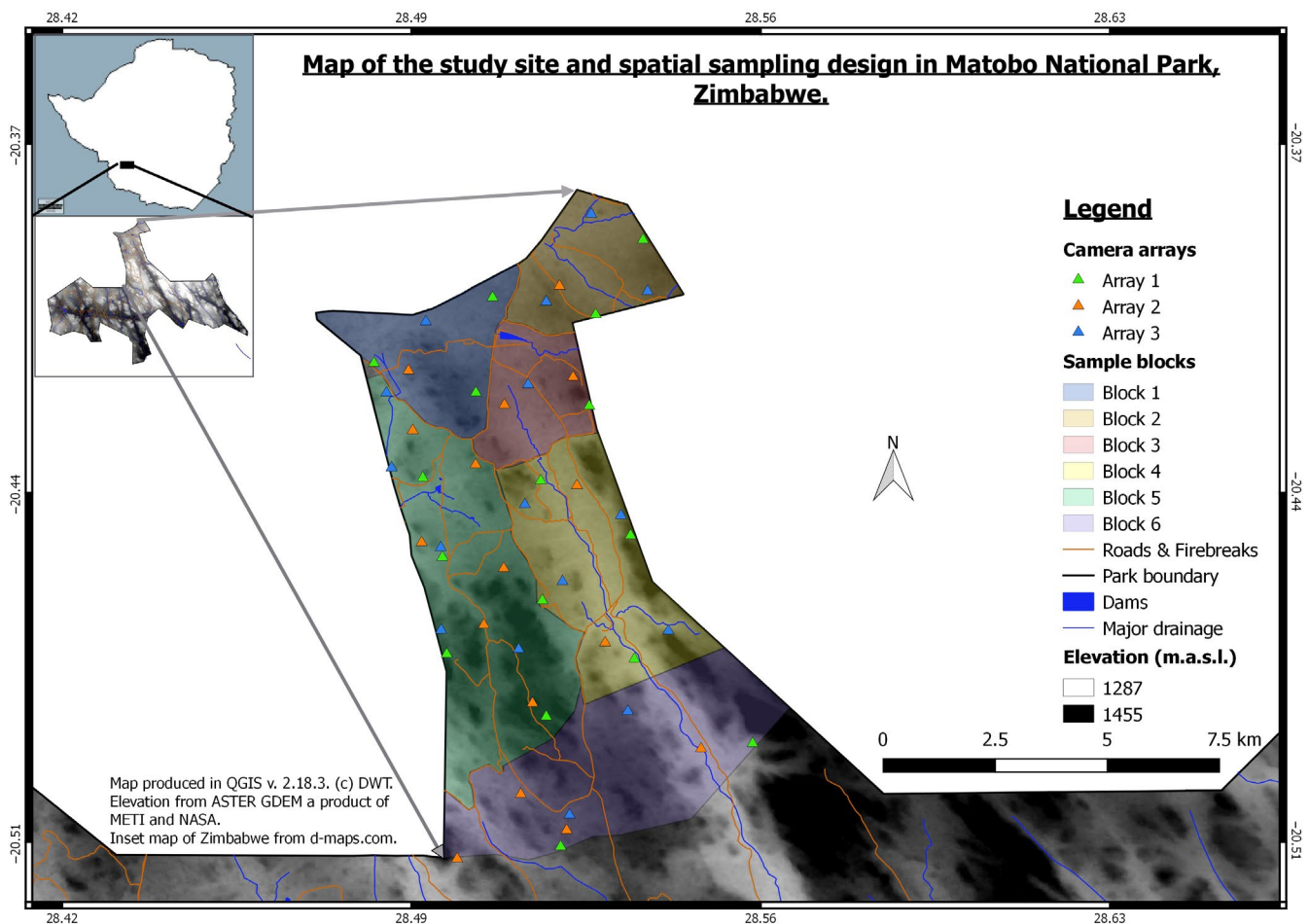


**FIGURE 1** Map showing the location of the study site and the spatial sampling design

*rotundifolius* and *Heteropyxis dehniae* (Kumirai et al., 2003), while in the valleys, open mixed woodland and grassland dominate (Kumirai et al., 2003; Lunt, 2011). *Colophospermum mopane* forms distinct almost monospecific patches, with a few tree species such as *Euclea divinorum*, *Terminalia randii* and *Pappea capensis* associated with it. The herbaceous layer is variously dominated by *Loudetia simplex*, *Hyperthelia dissoluta*, *Hyparrhenia* spp., *Andropogon* spp., *Eragrostis* spp., *Cymbopogon* spp., *Themeda triandra*, *Heteropogon contortus*, *Aristida* spp., *Pennisetum macrourum* and *Schizachyrium* spp.

## 2.2 | Data collection

Data were collected across all three seasons, that is hot dry (September–November 2016), hot wet (January–March 2017) and cool dry (May–July 2017). Nocturnal direct observations were not possible, due to safety concerns of tracking rhino on foot at night. We therefore investigated 24-hr activity patterns using continuously deployed camera traps and used direct observations to record detailed daytime behaviour allocations. We assumed that, within a season, the total time allocated to feeding and resting per 24-hr period would be relatively constant, based on probable similar energetic demands and forage quality and availability within the season. A previous study in Ziwa Sanctuary, Uganda, also reported consistent and predictable allocation of behaviours by white rhino per 24-hr period (Patton, Campbell, Genade, Ayiko, & Lutalo, 2011). Therefore, within a season changes in photographic captures with time of day would be indicative of changes in activity (e.g. travel and feeding) that may be linked with natural rhythms, for example, to phases of the moon, as has been found elsewhere (Yerushalmi & Green, 2009).

### 2.2.1 | Camera trapping

Forty-eight sampling sites, separated by at least 1.5 km, were selected using a random point selector in QGIS v. 2.14 (QGIS Development Team, 2016) to ensure adequate spatial coverage of the study area. Three arrays, each comprising 16 camera trap sites spread across the sampling area, were sampled sequentially for 20 days in each season (Figure 1). Camera sites used were located on foot, with cameras deployed at a utilised site (e.g. wildlife trail, rubbing post, drinking/wallowing site or grazing area) as close as possible to the randomly generated GIS point. Kopjes (steep-sided rocky outcrops) were excluded, due to their inaccessibility both for sampling and by white rhino. At each site, a single Bushnell TrophyCam® digital camera with infrared flash was attached to a secure tree at a height of one metre above ground. Cameras were set to maximum resolution (8 MP), with single images captured at 4-s trigger intervals. Photographs were downloaded after 20 days, and all white rhino images were extracted with date, time and location data. Since only a small percentage of photographs allowed identities of individuals to be determined, we defined a single, independent capture event as sequential photographs of white rhino, irrespective of number of individuals, obtained

within a 60-min period, as has been used elsewhere (Bowkett, Rovero, & Marshall, 2008). Measures of nocturnal illumination were not possible, as we did not have access to cloud cover data and we did not consider the amount of time the moon was visible above the horizon. However, natural behavioural rhythms linked to moon phase exist in a wide range of organisms (Yerushalmi & Green, 2009) including large mammals, so we investigated variations in white rhino activity periods across the phases of the moon. The moon phase for each capture event was then recorded, using standard nomenclature, that is new moon, first quarter (waxing), full moon and third quarter (waning).

### 2.2.2 | Direct observations

The study area was divided into six sampling blocks to obtain reasonable spatial coverage of the area (Figure 1). Blocks were of different sizes and were related to ranger patrol areas for operational efficiency; this allowed us to coordinate with rangers to locate rhino groups early in the morning for observation. Each block was visited no more than once during each week of observation, and observations were conducted for 4 weeks per season. White rhino in the area are continually monitored by the Zimbabwe Parks and Wildlife Management Authority (ZPWMA) for security reasons and are identified using ear notches. The ear notch system helped to distinguish herds and/or individuals to avoid sampling the same animals during the same week. Each sampling block was accessed by vehicle, while tracking was done on foot and commenced at 05h00 each day. If, by 08h00, no individuals had been located, or the tracked herd comprised individuals already observed that week, observations were abandoned for the day. Animals were observed from the time of encounter (earliest, 06h00) until 18h00, and observations were conducted using binoculars from a distance of ≥100 m to avoid disturbing their natural behaviour. The number of observation days and the number of individuals observed varied across seasons depending on the spatial distribution of animals and the composition of rhino herds. For security reasons, the total population size cannot be reported, but sampling effort comprised 13 individuals over 18 days of observation in the hot dry season, 19 individuals over 20 observation days in the hot wet season and 17 individuals over 19 observation days in the cool dry season.

During each observation period, binoculars (BARSKA 8 × 42 STORM EX) were used to accurately identify rhino ear notch patterns and record rhino behaviour. Scan sampling was used to record the behaviour of all individuals at 15-min intervals (Altmann, 1974). Behaviour was categorised as feeding, walking, lying down/resting, vigilance, social interaction and wallowing, following Bronikowski and Altmann (1996), Condy (1973) and Owen-Smith (1973; Table 1). Additional intermittent behaviours such as rubbing and drinking were also recorded.

Explanatory variables recorded were season; time; habitat type; the spatial coordinates of feeding, resting and wallowing sites (utilised sites only); distance to roads; moon phase; presence/absence of other mammals; herd composition; and behaviour. Distance to roads (in metres) was calculated as the mean of all the distances measured from

**TABLE 1** Ethogram for white rhino behaviour states used in this study

| Behaviour | Operational definition |
|---|---|
| Feeding | When an animal is in oral contact with food, exhibiting the consumption of food into its mouth |
| Walking | When an animal is moving with purpose such as towards water or between feeding sites and not feeding as it is moving |
| Socialising | When an individual white rhino interacts directly with another white rhino |
| Lying down/resting | When an animal is inactive and lying on the ground or standing motionless (with the head lowered down so that the lips are close or actually touching the ground) and not engaged in feeding or in social interactions |
| Vigilance | When an animal examines its surroundings in order to heighten awareness either with the head raised and ears focusing in different directions |
| Wallowing | When an animal lies in mud and/or in water |

closest roads for each site in Google Earth (Google Inc. 2017). Time of day was categorised into early morning (06h00–09h00), mid-morning (09h00–12h00), early afternoon (12h00–15h00) and late afternoon (15h00–18h00). Habitat type was categorised as open shrub, dense shrub, open woodland, dense woodland, mopane woodland, open grassland and reed bed (Table 2). Weather conditions were recorded using the degree of cloudiness and rain falling following Owen-Smith (1973). Herd composition recorded the identities (based on ear notches) of individuals and was summarised into territorial adult males, nonterritorial adult males, cow–calf herds irrespective of the presence of other individuals, and subadult herds. Age categories were defined as follows: juveniles—dependant calves (typically under 2.5 years old in MNP); subadults—independent immature animals up to 6.9 years old; and adults—fully grown animals over 7 years old. The presence/absence of other large mammals was recorded as either 1 (other mammals present) or 0 (no other mammals present).

## 2.3 | Statistical analysis

Camera trap records were separated into number of events recorded during the day (06h00–18h00) and night (18h00–06h00) under each of the four moon phases. The number of night-time captures was compared within and across seasons using chi-square tests.

For each day's observations, behavioural data were converted into a percentage per hour per individual and used to investigate associations between behaviour category and season, distance to roads (in metres; continuous), weather conditions, moon phase, presence/absence of other mammals (binary), time of day and herd composition. The percentage of observations recorded for each behavioural category was compared across predictor variables using the Kruskal–Wallis test, followed by a post hoc analysis using the PCMCR package (Pohlert, 2014) in R studio version 1.1.442 (R Core Team, 2017).

The association between the measured factors and white rhino behaviour was explored using a permutational multivariate analysis of variance (PERMANOVA; with 999 permutations) based on Bray–Curtis similarity using the vegan package (Oksanen et al., 2018). Individual identity and herd membership were included as covariates. PERMANOVA allows the partitioning of the total sum of squares and calculates a distance-based pseudo-$F$ statistic for each term in the model (Oksanen et al., 2018). $p$ values were obtained using a Monte Carlo significance test (999 permutations) for each term under the reduced model.

**TABLE 2** Habitat types (and their descriptions) recorded in Hazelside area during the study, based on a habitat map for the area (Gardner, 2015)

| Habitat type | Description |
|---|---|
| Open grassland | Open grasslands comprising tall grasses with no or very few trees (<5% cover) |
| Reed bed | Riverine areas predominantly covered by *Phragmites* and *Pennisetum* species |
| Open shrub | Areas covered by short, spaced multistemmed woody vegetation |
| Open woodland | All woodland areas with spaced trees characterised by separated tree canopies |
| Mopane woodland | Areas predominantly covered by *Colophospermum mopane* (both trees and shrubs) |
| Dense woodland | All woodland areas with trees closely spaced having overlapping or bordering tree canopies |
| Dense shrub | Areas covered by short, impenetrable multistemmed woody vegetation (>75%) closely spaced |

Canonical correspondence analysis (CCA), performed using Canoco version 4.5 (Ter Braak & Smilauer, 2002), was further used to explore the variation in white rhino behaviour and observed environmental variables. Only variables that were significantly associated with white rhino behaviour in the PERMANOVA were used in the CCA. Season, herd composition, individual identity of the observed animals and presence/absence of other mammals were therefore excluded in the CCA due to their low explanatory power. Variance partitioning, performed by partial CCA (Aarrestad et al., 2011), was used to explain the variation in the species data in relation to each factor and different sets of explanatory variables related to habitat attributes (habitat type and distance to roads), temporal attributes (time of day and moon phase), weather conditions and age/sex category. We assigned numeric classes to our non-numeric categorical variables. Habitat type was classified based on tree density as (a) reed bed, (b) open grassland, (c) open shrub, (d) open woodland, (e) mopane woodland, (f) dense shrub and (g) dense woodland. Weather conditions were based on sunlight intensity: (a) rainy, (b) cloudy and (c) sunny. Time of day was classified using a temperature proxy from cool to hot: (a) early morning, (b) late afternoon, (c) mid-morning and (d) early afternoon. Moon phase was classified as (a) new moon, (b) first quarter, (c) third quarter and (d) full moon. The age/sex of the animals was categorised as (a) adult males, (b) adult females, (c) subadult males, (d) subadult females, (e) juvenile males and (f) juvenile females.

# 3 | RESULTS

## 3.1 | The influence of moon phase on diurnal and nocturnal activity

A total of 960 camera trap days were obtained in each season. The number of days obtained for each moon phase period within each season was similar (chi-square test $\chi^2 = 24$, $p = .155$). Diurnal capture events for rhino (mean $\pm$ SE) were significantly different between the new (1.55 $\pm$ 0.03), first quarter (0.78 $\pm$ 0.02), full (0.28 $\pm$ 0.01) and third quarter (0.37 $\pm$ 0.01) moon phase days (chi-square test $\chi^2 = 54.448$, $p < .001$). Night-time capture events were significantly higher during the full moon periods (1.39 $\pm$ 0.03) than other moon phases ($\chi^2 = 58.544$, $p = .004$). However, there was no significant relationship detected between season and diurnal (chi-square test $\chi^2 = 11.648$, $p = .7679$) and nocturnal (chi-square test $\chi^2 = 15.167$, $p = .855$) number of capture events.

## 3.2 | Patterns in white rhino behaviour

Direct diurnal observations totalled 54 days (588 hr) across all seasons, with a total of 20 different individuals observed. Behavioural patterns of white rhino varied significantly with habitat type, distance to roads, weather conditions, moon phase, age/sex category and time of day, but not with season, herd composition, individual identity of the animal(s) or presence/absence of other mammals (PERMANOVA test; Table 3). We applied variance partitioning to determine the contribution of the environmental variables to variation in white rhino behavioural patterns.

The results of a CCA of the relationship between rhino behaviour and environmental variables are shown in Figure 2. Measured environmental variables explained 98.6% of the total variation in white rhino behavioural patterns (Figure 2). A Monte Carlo unrestricted permutation test (999 permutations) indicated that axis 1 and axis 2 were statistically significant ($p < .001$). Weather conditions accounted for the majority of variation in behaviour apportionment among the measured variables, followed by time of day, moon phase, habitat type, distance to roads and age/sex category of the animals (Table 4). Variance partitioning by sets of explanatory variables indicated that weather conditions had the greatest explanatory power of the variation in white rhino behaviour, followed by temporal attributes, habitat attributes and finally age/sex of the animals (Table 5).

**TABLE 3** Results of a permutational multivariate analysis of variance (PERMANOVA) of the effects of different environmental variables on the behavioural patterns of white rhino in Matobo National Park, Zimbabwe

| Source of variation | df | SS | MS | F.Model | $R^2$ | p value |
|---|---|---|---|---|---|---|
| Season | 2 | 0.70 | 0.14 | 1.23 | .00 | .291 |
| Habitat type | 6 | 122.28 | 20.38 | 179.59 | .28 | **.001** |
| Distance to roads | 1 | 2.36 | 2.36 | 20.80 | .01 | **.001** |
| Weather conditions | 2 | 85.92 | 42.96 | 378.60 | .20 | **.001** |
| Moon phase | 3 | 8.85 | 2.95 | 26.00 | .02 | **.001** |
| Herd composition | 2 | 0.03 | 0.03 | 0.25 | .00 | .578 |
| Time of day | 3 | 25.47 | 8.49 | 74.81 | .06 | **.001** |
| Presence/absence of other mammals | 1 | 0.04 | 0.04 | 0.84 | .00 | .271 |
| Age/sex category | 5 | 0.71 | 0.71 | 6.23 | .00 | **.011** |
| Individual identity | 19 | 2.73 | 0.144 | 1.27 | .00 | .147 |

*Note:* Significant p values appear in bold.

Abbreviations: df, degrees of freedom; MS, mean squares; SS, sum of squares.

**FIGURE 2** Canonical correspondence analysis (CCA) biplot diagram (first two axes explaining 98.6% of total variation) of environmental variables and white rhino behaviour patterns (centroids) in Matobo National Park, Zimbabwe
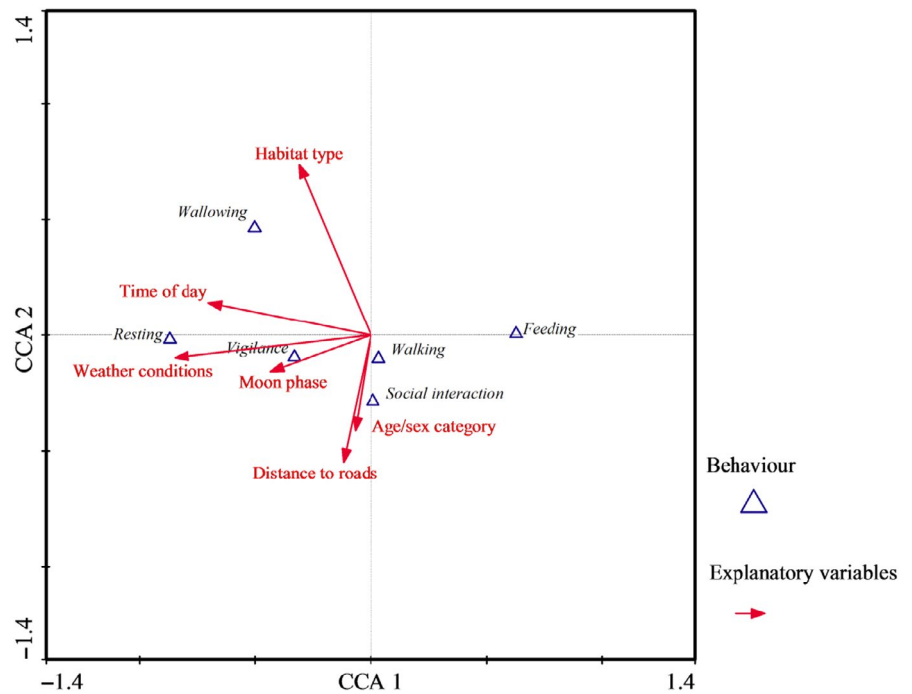


**TABLE 4** The percentage variation ($V$) in the species data explained by the environmental variables in a canonical correspondence analysis (CCA) of white rhino behavioural ecology data in Matobo National Park, Zimbabwe, estimated with two different methods: $V_1$ marginal effects (one variable at a time) and $V_2$ conditional effects (forward selection of variables)

| Variable | $\lambda_1$ | $V_1$ | $\lambda_2$ | $V_2$ |
|---|---|---|---|---|
| Weather conditions | 0.35*** | 13.86 | 0.35*** | 60.41 |
| Time of day | 0.24*** | 9.50 | 0.12*** | 20.65 |
| Moon phase | 0.09*** | 3.56 | 0.06*** | 10.33 |
| Habitat type | 0.05*** | 1.98 | 0.03*** | 5.16 |
| Distance to roads | 0.01*** | 0.40 | 0.01*** | 1.72 |
| Age/sex category | 0.01*** | 0.40 | 0.01*** | 1.72 |

*Note:* $\lambda_1$ = eigenvalue of the first axis in a CCA with the one environmental variable.

$V_1 = [\lambda_1/\text{sum of all unconstrained eigenvalues in a CA, total inertia}] \times 100$ (percentage variation in the species data explained by the environmental variable alone, marginal effects).

$\lambda_2$ = eigenvalue of the first axis in a CCA with forward selection of the environmental variables.

$V_2 = [\lambda_2/\text{sum of all canonical eigenvalues in a CCA}] \times 100$ (percentage variation in the species data explained by the variable in a forward selection where the variation explained by the more important variables is removed, conditional effects).

***Significant ($p \leq .001$), as obtained in Monte Carlo permutation tests (999 unrestricted permutations).

**TABLE 5** Variation in diurnal behaviour of white rhino (in percentage) explained by sets of variables related to weather conditions (A), temporal attributes (B), habitat attributes (C) and age/sex category (D) by methods of variance partitioning in Matobo National Park, Zimbabwe

| Subset I | Subset II | $V_1$ | $V_2$ | $V_3$ | $V_t$ | $V_u$ |
|---|---|---|---|---|---|---|
| A. Weather conditions | (B + C + D) | 26.54 | 18.20 | 13.36 | 58.1 | 41.9 |
| B. Temporal attributes | (A + C + D) | 15.27 | 19.59 | 23.24 | 58.1 | 41.9 |
| C. Habitat attributes | (A + B + D) | 2.32 | 15.96 | 39.82 | 58.1 | 41.9 |
| D. Age/sex category | (A + B + C) | 0.58 | 9.23 | 48.29 | 58.1 | 41.9 |

*Note:* $V_1$: variation explained by subset I, when variation due to subset II is allowed for statistically (as covariables); $V_2$: variation shared by subsets I and II; $V_3$: variation explained by subset II, when variation due to subset I is allowed for statistically (as covariables); $V_t$: total variation explained by the variables (both subset I and subset II); $V_u$: the unexplained variation.

TABLE 6   Mean ± standard error observations (%) on various behaviours by white rhino in Matobo National Park, Zimbabwe, across different moon phases

| Behaviour | New moon | 1st Quarter | Full moon | 3rd Quarter |
|---|---|---|---|---|
| Feeding | $71.53 \pm 0.11^a$ | $63.57 \pm 0.09^b$ | $31.93 \pm 0.10^c$ | $48.99 \pm 0.14^d$ |
| Resting | $19.72 \pm 0.12^a$ | $25.29 \pm 0.16^b$ | $53.89 \pm 0.11^c$ | $40.09 \pm 0.09^d$ |
| Social interaction | $2.29 \pm 0.41$ | $1.42 \pm 0.01$ | $2.53 \pm 0.02$ | $2.59 \pm 0.19$ |
| Walking | $2.50 \pm 0.02$ | $2.88 \pm 0.03$ | $3.15 \pm 0.02$ | $2.98 \pm 0.04$ |
| Wallowing | $2.29 \pm 0.04$ | $4.18 \pm 0.04$ | $4.90 \pm 0.04$ | $2.53 \pm 0.03$ |
| Vigilance | $1.67 \pm 0.02$ | $2.66 \pm 0.02$ | $3.60 \pm 0.03$ | $2.82 \pm 0.02$ |

*Note:* Means not sharing a common letter within each row differed significantly ($p < .05$).

TABLE 7   Mean ± standard error observations (%) on various behaviours by white rhino during the day in Matobo National Park, Zimbabwe

| Behaviour | Early morning | Mid-morning | Early afternoon | Late afternoon |
|---|---|---|---|---|
| Feeding | $80.92 \pm 0.08^a$ | $26.79 \pm 0.09^b$ | $29.79 \pm 0.10^b$ | $77.48 \pm 0.09^c$ |
| Resting | $10.36 \pm 0.06^a$ | $64.13 \pm 0.11^b$ | $57.33 \pm 0.11^b$ | $10.17 \pm 0.07^a$ |
| Social interaction | $3.20 \pm 0.02$ | $3.19 \pm 0.02$ | $1.36 \pm 0.01$ | $1.81 \pm 0.03$ |
| Walking | $3.14 \pm 0.02$ | $2.96 \pm 0.01$ | $2.60 \pm 0.02$ | $2.70 \pm 0.02$ |
| Wallowing | $0.0^a$ | $0.0^a$ | $6.44 \pm 0.04^b$ | $6.19 \pm 0.06^c$ |
| Vigilance | $2.38 \pm 0.01$ | $2.93 \pm 0.03$ | $2.48 \pm 0.02$ | $1.65 \pm 0.02$ |

*Note:* Means not sharing a common letter within each row differed significantly ($p < .05$).

Interaction effects also accounted for some of the observed variation (Table 5).

The first axis on the CCA biplot ordination diagram (Figure 2) represented a gradient in behaviour categories in relation to weather conditions, moon phase, time of day and habitat type, while variation along the second axis was related primarily to age/sex category of the animal(s) and distance to roads. Feeding behaviour was positively associated with new and first-quarter moon phases, early morning and late afternoon periods, cloudy weather and open shrub habitats (Figure 2). There was a negative association between feeding behaviour and distance to roads, sunny weather, full- and third-quarter moon phases, the early afternoon period, and mopane woodland and open woodland habitats (Figure 2). By contrast, resting behaviour was positively associated with the mid-morning and early afternoon periods, sunny weather, increased distance to roads, full moon, and mopane woodland and open woodland habitats (Figure 2). Wallowing was positively associated with sunny weather conditions, late afternoon and mopane habitat where sodic soils supported mud wallows. White rhino social interaction indicated a strong association with adult females and immature (juveniles and subadults) animals (Figure 2). Walking and vigilance behaviours were more frequently associated with solitary adult males.

Weather conditions significantly influenced feeding duration, that is percentage of observations (mean ± *SE*; Kruskal–Wallis $\chi^2 = 826.26$, $p < .001$), with more than twice as much day time spent feeding in cloudy ($84.51 \pm 0.03\%$) and rainy ($79.65 \pm 0.77\%$) weather than during sunny conditions ($18.28 \pm 0.05\%$) throughout the study. The percentage of observations for resting behaviour (mean ± *SE*) was significantly higher in sunny weather ($67.44 \pm 0.05\%$) compared to cloudy weather conditions ($6.48 \pm 0.03\%$; Kruskal–Wallis

$\chi^2 = 772.31$, $p < .001$). Diurnal wallowing was observed during the hot wet season only and was more prevalent in rainy ($5.19 \pm 2.46\%$) and sunny ($5.14 \pm 1.03\%$) weather than in cloudy conditions ($0.76 \pm 0.42\%$; Kruskal–Wallis $\chi^2 = 21.158$, $p < .001$). Weather conditions did not significantly influence time allocation to social interaction (Kruskal–Wallis $\chi^2 = 2.692$, $p = .260$), walking (Kruskal–Wallis $\chi^2 = 0.680$, $p = .712$) or vigilance behaviour (Kruskal–Wallis $\chi^2 = 4.782$, $p = .218$).

Only the percentage of observations recorded for feeding and resting differed significantly with moon phase ($p < .001$; Table 6). Feeding behaviour was most prevalent during new moon, followed by first quarter and third quarter, and lastly full moon (Kruskal–Wallis $\chi^2 = 165.78$, $p < .001$). In contrast, white rhino rested significantly more (>50% of the day) during full moon than other moon phases (Kruskal–Wallis $\chi^2 = 152.23$, $p < .001$). There were no significant differences in the percentage of observations of other behaviours across moon phases (social interaction: Kruskal–Wallis $\chi^2 = 4.354$, $p = .226$; walking: Kruskal–Wallis $\chi^2 = 6.472$, $p = .091$; wallowing: Kruskal–Wallis $\chi^2 = 7.044$, $p = .139$; and vigilance: Kruskal–Wallis $\chi^2 = 8.097$, $p = .044$; Table 6).

Overall, rhinos dedicated most of the daytime (mean ± *SE*) to feeding ($53.07 \pm 0.08\%$) and resting ($35.40 \pm 0.05\%$), with walking ($3.04 \pm 0.03\%$), vigilance behaviour ($2.71 \pm 0.01\%$), social interaction ($2.24 \pm 0.01\%$) and wallowing ($3.54 \pm 0.02\%$; only in the hot wet season) contributing less than 15% to the diurnal activity budget. Significantly more time, that is percentage of observations (mean ± *SE*), was spent feeding in the morning and late afternoon than during other periods (Kruskal–Wallis $\chi^2 = 533.46$, $p < .001$, Table 7). The converse was true for resting, which was prevalent in the hotter periods of mid-morning and early afternoon (Kruskal–Wallis $\chi^2 = 523.68$, $p < .001$). Wallowing occurred significantly

more in the late afternoon compared to the other times of the day (Kruskal–Wallis $\chi^2 = 102.83$, $p < .001$; Table 7). Vigilance (Kruskal–Wallis $\chi^2 = 9.697$, $p = .061$), walking (Kruskal–Wallis $\chi^2 = 5.483$, $p = .094$) and social interactions (Kruskal–Wallis $\chi^2 = 3.412$, $p = .581$) were independent of time of day.

White rhino feeding varied significantly with habitat type (Kruskal–Wallis $\chi^2 = 570.2$, $p < .001$) with the percentage of feeding observations (mean $\pm$ *SE*) being highest in open shrub (81.71 $\pm$ 0.05%) habitat followed by dense shrub (78.49 $\pm$ 0.28%), reed bed (73.53 $\pm$ 1.21%) and dense woodland (69.79 $\pm$ 0.44%). Resting behaviour occurred significantly more frequently in mopane woodland (64.10 $\pm$ 0.17%) and open woodland (56.05 $\pm$ 0.08%) habitat types (Kruskal–Wallis $\chi^2 = 447.46$, $p < .001$). Wallowing was more frequent in mopane woodland (14.66 $\pm$ 0.11%; Kruskal–Wallis $\chi^2 = 168.16$, $p < .001$), where sodic soils supported mud wallows, than in other habitats. No clear association with habitat was found for social interaction (Kruskal–Wallis $\chi^2 = 3.87$, $p = .731$), walking (Kruskal–Wallis $\chi^2 = 9.01$, $p = .235$) or vigilance (Kruskal–Wallis $\chi^2 = 1.61$, $p = .906$).

Social interaction was frequently exhibited between cows (2.41 $\pm$ 0.02%, $n = 540$) and juveniles (i.e. juvenile females: 3.04 $\pm$ 0.03%, $n = 312$; juvenile males: 3.75 $\pm$ 0.04, $n = 240$) compared with subadults with each other (1.51 $\pm$ 0.02%, $n = 348$; Kruskal–Wallis $\chi^2 = 41.87$, $p < .001$). Solitary males devoted more time to walking and marking territories (8.5 $\pm$ 0.05%, $n = 180$) compared to other individuals (Kruskal–Wallis $\chi^2 = 38.21$, $p < .001$). The percentage of observations recorded for feeding by white rhino was highest among herds of subadults (60.75 $\pm$ 5.47%), followed by cows and juveniles (58.05 $\pm$ 2.18%) and solitary adult males (55.19 $\pm$ 3.25%; Kruskal–Wallis $\chi^2 = 11.521$, $p = .021$).

# 4 | DISCUSSION

Using variance partitioning based on marginal and conditional effects, we demonstrated that variation in temporal, weather conditions and habitat attributes and their interactions influenced the amount of time white rhino allocated to various behaviours during the day. Temporal, weather and habitat factors together influenced the timing of behaviours over the day. Behaviour type varied with habitat, and age/sex of the animals influenced the apportionment of time to behaviours. Feeding, resting and seasonal wallowing comprised the bulk of daytime behaviours exhibited, with travel, social interactions and vigilance typically contributing less than 13% to the diurnal activity budget. Camera trap data contributed useful insights into diurnal and nocturnal activity patterns, justifying the inclusion of moon phase in diurnal behaviour pattern analyses.

## 4.1 | Temporal and weather effects on white rhino activity budgets

White rhino and other large-bodied mammals have high thermal inertia which limits their ability to lose heat rapidly (du Toit &

Yetman, 2005; Owen-Smith, 1988), but high energetic requirements and dispersed forage require them to feed for a substantial part of the diel cycle (Owen-Smith, 1973). It would therefore be expected that active behaviours, such as feeding, travel and territorial defence, would be restricted to cooler periods for thermoregulatory reasons (Condy, 1973; Monks, 1995; Owen-Smith, 1973; van Gyseghem, 1984). This was borne out by our data, with significant variation in the allocation of daytime to feeding and resting associated with moon phase, time of day and weather conditions. The lack of a seasonal effect on activity budgets as demonstrated by PERMANOVA was unexpected, but may be explained by the confounding effects of variable temperatures and weather within seasons. Patton et al. (2011) also reported predictable time allocations, which may suggest a degree of inflexibility in overall activity budgets in white rhino.

Moon phase affects nocturnal behaviour patterns in mammals (Wronski, Apio, & Plath, 2006), with a number of studies finding ungulates to be more active during full moon nights when visibility is improved (Packer, Swanson, Ikanda, & Kushnir, 2011; Prugh & Golden, 2014; Traill, Martin, & Owen-Smith, 2016; Wronski et al., 2006). Although we did not conduct nocturnal observations, it is reasonable to assume that over a 24-hr period, foraging time would be relatively constant to meet energetic demands. Camera trap records showed increased nocturnal activity and decreased diurnal activity during full moon, irrespective of season, which suggests that active behaviours (including feeding) were preferentially conducted at night when it was moonlit and cooler. Thus, the observation of reduced daytime foraging and increased resting when the moon was full may be due to differential nocturnal activity. Predation risk in MNP is also low, offering few constraints to nocturnal activities (Owen-Smith, 1988).

Thermoregulation was probably also a primary determinant of allocation of behaviours across the day and with variation in weather (Condy, 1973; Monks, 1995; Owen-Smith, 1973, 1988; van Gyseghem, 1984). Active behaviours, such as feeding and walking, prevailed during the cooler early and late hours of the day, but extended into the mid-morning and early afternoon periods when it was overcast or raining; in fact, more than twice as much time during the day was spent feeding in overcast and rainy conditions than when it was sunny. Resting behaviour predominated in the hotter hours of the day, with white rhino selecting well-shaded habitats with good visibility (e.g. open mopane woodland) to sleep in. In the hot wet season, mud-wallowing, which probably had both thermoregulatory and parasite-reducing functions (Owen-Smith, 1973, 1988), was undertaken primarily on sunny afternoons during the habitual rest period and alternated with feeding in direct sunshine. The absence of mud-wallowing in other seasons may have been due to drying up of wallows in preferred sodic soils, but Owen-Smith (1973) also found that little wallowing took place during the dry season, even when mud of preferred consistency was available. Ectoparasite loads tend to be lower in the cooler and drier months (Owen-Smith, 1973), suggesting that the thermoregulatory benefits of wallowing may be secondary to parasite control in white rhino; the hottest month in MNP (October)

is towards the end of the hot dry season, and no mud-wallowing was recorded in that month. Routine, relatively low-cost behaviours, such as social interaction and vigilance, showed little variation with time of day and moon phase, although vigilance was slightly higher in the mid-morning period when rhinos were settling down to sleep.

## 4.2 | Effects of habitat attributes on diurnal activity budgets of white rhino

The amount of benefits that animals can derive from a particular habitat and its features influence the amount of time that animals will spend there (Perrin & Brereton-Stiles, 1999). Thus, animals are expected to spend more time in habitats characterised by higher resource availability (Shrader, 2003). White rhino in MNP showed distinct habitat preferences for feeding, resting and wallowing but not for ephemeral or reactionary behaviours such as social interactions or vigilance.

Selection of habitat for feeding was variable within and among seasons and might have been linked to forage quality (e.g. sward composition) and quantity (Owen-Smith, 1988). White rhino in the Hazelside area utilised open shrub habitats year-round, but utilisation of other habitats varied over the year with a general increase in the range of habitats used in the lean season, as has been found in other studies (Owen-Smith, 1973, 1988). Open grassland was traversed rather than being utilised for feeding, and the time dedicated to vigilance in grasslands was higher than in any other habitat type in this study.

Open woodland, including mopane-dominated woodland, was associated with resting. It is probable that the shade produced by large trees and better visibility due to the short sward reduced the energetic costs of thermoregulation and vigilance, respectively. Wallowing behaviour was also strongly linked with mopane woodland, where sodic soils retained water and provided mud of a preferred consistency (Owen-Smith, 1973).

Another feature of human-influenced landscapes is disturbance, such as vehicular traffic and walking safaris. Disturbance can result in the modification of behavioural patterns and individual performance of large mammals (Baker & Leberg, 2018; Caro, 1999; Frid & Dill, 2002; Pépin, Lamerenx, Chadelaud, & Recarte, 1996) by imposing limitations to movement (Klar, Herrmann, & Kramer-Schadt, 2009), affecting mating opportunities (Frair, Merrill, Beyer, & Morales, 2008; Leblond, Dussault, & Ouellet, 2013), modifying foraging routes (Leblond et al., 2013) or increasing perceived predation risk (Frid & Dill, 2002). Both spatial and temporal changes have been recorded, for example large-bodied mammals avoiding roads (Mohd-Azlan et al., 2018) or animals being active when humans are absent (Gaynor, Hojnowski, Carter, & Brashares, 2018). In our study, we considered the road network as a source of disturbance. Distance to roads was positively correlated with resting behaviour, despite suitable habitat being available close to roads. This infers that white rhino selected less disturbed sites to sleep. By contrast, rhinos preferred feeding sites close to roads possibly due to disturbance (animal movement and foraging) promoting plant species richness and diversity (i.e. the intermediate disturbance hypothesis, Weithoff, 2001) and possibly improved accessibility. The continued

use of sites close to roads increases sward attractiveness driving a positive feedback loop that ultimately results in the maintenance of grazing lawns (Owen-Smith, 1988). The use of feeding sites close to roads also suggests that white rhino may not consider roads as a landscape barrier.

## 4.3 | The influence of age, sex and herd composition on the activity budget

Behaviour can be expected to vary with the age and sex of individuals and the composition of herds, as social and physiological requirements differ. In this study, subadults—which are still actively growing and therefore have high energetic requirements—spent more time feeding than adults, similar to findings by Owen-Smith (1973). Solitary territorial bulls spent more time travelling than other demographic groups and were obviously the only category to be observed scent-marking, since only males mark and defend territories (Rachlow, Kie, & Berger, 1999). The greatest time allocation to social interaction was recorded among adult cows and dependant offspring. Little social interaction was recorded in herds of subadults in this study, possibly because these individuals were unrelated and, unlike mother–calf associations, did not form strong bonds (Shrader & Owen-Smith, 2002).

## 4.4 | Recommendations for management

Results of this study suggest that white rhino utilise a range of habitats over an annual cycle, which makes the maintenance of a mosaic of habitats an important consideration. Water distribution, except in exceptional drought years, is unlikely to be limiting in the Hazelside section, as distance between water points (natural sources and dams) was typically less than 5 km, which is a rule-of-thumb travel estimate for medium-to-large herbivores (Owen-Smith, 1996). Selection of resting sites was linked to habitats with good shade and good visibility (e.g. mopane stands) that were subject to little vehicular disturbance. Therefore, the planning of new access points, for example firebreaks and roads, should take this into account to ensure that there are sufficient resting refuges for white rhino.

## 5 | CONCLUSIONS

As demonstrated by the CCA using marginal and conditional effects, we conclude that the diurnal behaviour of white rhino in MNP is strongly influenced by weather conditions, followed by temporal attributes, habitat characteristics and age/sex of the animals. Temperature (within a day cycle) appeared to be the primary determinant in the timing of behaviours, with white rhino limiting active behaviours when it was hot. Habitat type and time of day (a proxy for temperature) interacted by influencing the activities rhinos engaged in over the day; thus, habitats with shade and good visibility were selected during the heat of the day for resting, while those

providing good forage quality and quantity were preferred for feeding during the cooler hours. Soils that provided ideal mud consistency for wallowing attracted white rhino during hot, wet weather when thermoregulation and parasite control were important. Finally, behaviour apportionment varied with age or sex of the animals because of different energetic and social requirements; calves and mothers interacted more than unrelated animals, bulls needed to maintain territories, and subadults spent more time feeding to meet high energetic requirements for growth.

## ACKNOWLEDGEMENTS

## CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

## ETHICAL APPROVAL

All applicable international, national and/or institutional guidelines for the care and use of animals were followed.

## DATA AVAILABILITY STATEMENT

The data sets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

## ORCID

*Tafadzwa Tichagwa* 🆔 https://orcid.org/0000-0001-6802-0380

*Hilton G. T. Ndagurwa* 🆔 https://orcid.org/0000-0002-9349-6548

## REFERENCES

Aarrestad, P. A., Masunga, G. S., Hytteborn, H., Pitlagano, M. L., Marokane, W., & Skarpe, C. (2011). Influence of soil, tree cover and large herbivores on field layer vegetation along a savanna landscape gradient in northern Botswana. *Journal of Arid Environments*, *75*(3), 290–297. https://doi.org/10.1016/j.jaridenv.2010.10.009

Altmann, J. (1974). Observational study of behaviour: Sampling methods. *Behaviour*, *49*, 227–267.

Baker, A. D., & Leberg, P. L. (2018). Impacts of human recreation on carnivores in protected areas. *PLoS One*, *13*(4), e0195436. https://doi.org/10.1371/journal.pone.0195436

Belovsky, G. E., & Slade, J. B. (1986). Time budgets of grassland herbivores: Body size similarities. *Oecologia*, *70*(1), 53–62. https://doi.org/10.1007/BF00377110

Bowkett, A. E., Rovero, F., & Marshall, A. R. (2008). The use of camera-trap data to model habitat use by antelope species in the Udzungwa mountain forests, Tanzania. *African Journal of Ecology*, *46*(4), 479–487. https://doi.org/10.1111/j.1365-2028.2007.00881.x

Bronikowski, A. M., & Altmann, J. (1996). Foraging in a variable environment: Weather patterns and the behavioral ecology of baboons. *Behavioral Ecology and Sociobiology*, *39*(1), 11–25. https://doi.org/10.1007/s002650050262

Caro, T. (1999). The behaviour-conservation interface. *Trends in Ecology and Evolution*, *14*(9), 366–369. https://doi.org/10.1016/S0169-5347(99)01663-8

Condy, P. R. (1973). *The population status, social behaviour and daily activity pattern of the white rhinoceros in Kyle National Park, Rhodesia*. M.Sc. thesis, University of Rhodesia.

du Toit, J. T., & Yetman, C. A. (2005). Effects of body size on the diurnal activity budgets of African browsing ruminants. *Oecologia*, *143*, 317–325. https://doi.org/10.1007/s00442-004-1789-7

Emslie, R. (2012). *Ceratotherium simum: Emslie, R.: The IUCN Red List of Threatened Species 2012: e.T4185A16980466*. https://doi.org/10.2305/IUCN.UK.2012.RLTS.T4185A16980466.en

Frair, J. L., Merrill, E. H., Beyer, H. L., & Morales, J. M. (2008). Thresholds in landscape connectivity and mortality risks in response to growing road networks. *Journal of Applied Ecology*, *45*(5), 1504–1513. https://doi.org/10.1111/j.1365-2664.2008.01526.x

Frid, A., & Dill, L. (2002). Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, *6*(1), 11. https://doi.org/10.5751/ES-00404-060111

Gardner, R. S. (2015). *Broadscale habitat map of Matobo National Park, Zimbabwe*, UK: [Map]. Marwell Wildlife.

Gaynor, K. M., Hojnowski, C. E., Carter, N. H., & Brashares, J. S. (2018). The influence of human disturbance on wildlife nocturnality. *Science*, *360*(6394), 1232. https://doi.org/10.1126/science.aar7121

Hutchins, M., & Kreger, M. D. (2006). Rhinoceros behaviour: Implications for captive management and conservation. *International Zoo Yearbook*, *40*(1), 150–173. https://doi.org/10.1111/j.1748-1090.2006.00150.x

Jordaan, H., Brown, L. R., & Slater, K. (2015). Habitat utilization of white rhinoceros (*Ceratotherium simum simum*) on Willem Pretorius Game Reserve, Free-State Province, South Africa. *Pachyderm*, *56*, 61–71.

Kiwia, H. Y. D. (1989). Ranging patterns of the black rhinoceros (*Diceros bicornis* L.) in Ngorongoro Crater, Tanzania. *African Journal of Ecology*, *27*, 305–312. https://doi.org/10.1111/j.1365-2028.1989.tb01024.x

Klar, N., Herrmann, M., & Kramer-Schadt, S. (2009). Effects and mitigation of road impacts on individual movement behaviour of wildcats. *Journal of Wildlife Management*, *73*(5), 631–638.

Kumirai, A., Msimanga, A., Munyikwa, D., Chidavaenzi, R., & Muringaniza, S. J. (2003). *Nomination Dossier for the proposed Matobo Hills World Heritage*. UNESCO.

Leblond, M., Dussault, C., & Ouellet, J.-P. (2013). Impacts of human disturbance on large prey species: Do behavioral reactions translate to fitness consequences? *PLoS One*, *8*(9), e73695. https://doi.org/10.1371/journal.pone.0073695

Leuthold, B. M., & Leuthold, W. (1978). Daytime activity patterns of gerenuk and giraffe in Tsavo National Park, Kenya. *African Journal of Ecology*, *16*(4), 231–243. https://doi.org/10.1111/j.1365-2028.1978.tb00444.x

Leuthold, W. (1977). *African ungulates: A comparative review of their ethology and behavioral ecology*, NY: Springer.

Lunt, N. (2011). *The role of small antelope in ecosystem functioning in the Matobo Hills, Zimbabwe*. PhD. thesis, Rhodes University.

Mehradadfar, F. (1999). Behavioral activity budget of black rhino (Diceros bicornis bicornis) at a watering place. *Animal Keepers' Forum*, *26*, 358–368.

Mohd-Azlan, J., Kaicheen, S. S., & Yoong, W. C. (2018). Distribution, relative abundance and occupancy of selected mammals along paved road in Kubah National Park, Sarawak, Borneo. *Nature Conservation Research*, *3*(2). https://doi.org/10.24189/ncr.2018.028

Monks, N. J. (1995). *The population status, diurnal activity patterns, range and territory size, and habitat use by the white rhinoceros (Ceratotherium simum) in Kyle Recreational Park, Zimbabwe*. Msc thesis, University of Kent.

Notarbartolo-di-Sciara, G., Hanafy, M. H., Fouda, M. M., Afifi, A., & Costa, M. (2009). Spinner dolphin (*Stenella longirostris*) resting habitat

in Samadai Reef (Egypt, Red Sea) protected through tourism management. *Journal of the Marine Biological Association of the United Kingdom*, *89*(1), 211–216. https://doi.org/10.1017/S0025315408002221

O'Connor, S. A. M. (1986). Activity cycles of Southern white rhinoceros (*Ceratotherium simum*) in captivity: Implications for management. *International Zoo Yearbook*, *24*(25), 297–303.

Oksanen, J., Guillaume Blanchet, F., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., ... Wagner, H. (2018). *Vegan: Community Ecology Package. (R package version 2.4-6.) [Computer software]*. Retrieved from https://CRAN.R-project.org/package=vegan

Owen-Smith, N. (1973). *The behavioural ecology of the white rhinoceros*. PhD thesis, University of Wisconsin.

Owen-Smith, N. (1988). *Megaherbivores: The influence of very large body size on ecology*, NY: Cambridge University Press.

Owen-Smith, N. (1996). Ecological guidelines for waterpoints in extensive protected areas. *South African Journal of Wildlife Research*, *6*, 107–112.

Owen-Smith, N., & Goodall, V. (2014). Coping with savanna seasonality: Comparative daily activity patterns of African ungulates as revealed by GPS telemetry. *Journal of Zoology*, *293*(3), 181–191. https://doi.org/10.1111/jzo.12132

Packer, C., Swanson, A., Ikanda, D., & Kushnir, H. (2011). Fear of darkness, the full moon and the nocturnal ecology of African lions. *PLoS One*, *6*(7), e22285. https://doi.org/10.1371/journal.pone.0022285

Patton, F. J., Campbell, P. E., Genade, A., Ayiko, R., & Lutalo, G. (2011). The behaviour of white rhinos at Ziwa Rhino Sanctuary, Uganda with particular reference to night-time activity. *Pachyderm*, *50*, 77–83.

Pépin, D., Lamerenx, F., Chadelaud, H., & Recarte, J.-M. (1996). Human-related disturbance risk and distance to cover affect use of montane pastures by Pyrenean chamois. *Applied Animal Behaviour Science*, *46*, 217–228. https://doi.org/10.1016/0168-1591(95)00661-3

Perrin, M. R., & Brereton-Stiles, R. (1999). Habitat use and feeding behaviour of the buffalo and white rhinoceros in the Hluhluwe-Umfolozi Game Reserve. *South African Journal of Wildlife Research*, *29*, 71–80.

Pohlert, T. (2014). *The Pairwise Multiple Comparison of Mean Ranks Package (PMCMR)*. R package. Retrieved from https://cran.r-project.org/package=PMCMR

Prugh, L. R., & Golden, C. D. (2014). Does moonlight increase predation risk? Meta-analysis reveals divergent responses of nocturnal mammals to lunar cycles. *Journal of Animal Ecology*, *83*(2), 504–514. https://doi.org/10.1111/1365-2656.12148

QGIS Development Team. (2016). QGIS Geographic Information System v. 2.18 'Las Palmas'. Retrieved from http://qgis.osgeo.org

R Core Team. (2017). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Rachlow, J. L. (1997). *Demography, behavior, and conservation of white rhinos*. PhD thesis, University of Nevada Reno.

Rachlow, J. L., Kie, J. G., & Berger, J. (1999). Territoriality and spatial patterns of white rhinoceros in Matobo National Park, Zimbabwe. *African Journal of Ecology*, *37*, 295–304. https://doi.org/10.1046/j.1365-2028.1999.00175.x

Shi, J., Dunbar, R. I. M., Buckland, D., & Miller, D. (2003). Daytime activity budgets of feral goats (*Capra hircus*) on the Isle of Rum: Influence of season, age, and sex. *Canadian Journal of Zoology*, *81*(5), 803–815. https://doi.org/10.1139/z03-055

Shrader, A. M. (2003). *Use of food and space by white rhinos*. PhD Thesis, Faculty of Science, University of the Witwatersrand, Johannesburg.

Shrader, A., & Owen-Smith, N. (2002). The role of companionship in the dispersal of white rhinoceroses (*Ceratotherium simum*). *Behavioral Ecology and Sociobiology*, *52*(3), 255–261. https://doi.org/10.1007/s00265-002-0506-y

Ter Braak, C. J., & Smilauer, P. (2002). *CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (version 4.5)*. Retrieved from www.canoco.com

Traill, L. W., Martin, J., & Owen-Smith, N. (2016). Lion proximity, not moon phase, affects the nocturnal movement behaviour of zebra and wildebeest. *Journal of Zoology*, *299*(3), 221–227. https://doi.org/10.1111/jzo.12343

van Gyseghem, R. (1984). Observations on the ecology and behaviour of the northern white rhinoceros (*Ceratotherium simum cottoni*). *Zeitschrift Fur Saugetierkunde*, *49*, 348–358.

Wardjomto, M. B. (2013). *Feeding patch selection by white rhinoceros*. M. Tech., Tshwane University of Technology.

Weithoff, G. (2001). The intermediate disturbance hypothesis—Species diversity or functional diversity? *Journal of Plankton Research*, *23*(10), 1147–1155. https://doi.org/10.1093/plankt/23.10.1147

Wronski, T., Apio, A., & Plath, M. (2006). Activity patterns of bushbuck (*Tragelaphus scriptus*) in Queen Elizabeth National Park. *Behavioural Processes*, *73*(3), 333–341. https://doi.org/10.1016/j.beproc.2006.08.003

Yerushalmi, S., & Green, R. M. (2009). Evidence for the adaptive significance of circadian rhythms. *Ecology Letters*, *12*(9), 970–981. https://doi.org/10.1111/j.1461-0248.2009.01343.x