Climate and predation drive variation of diel activity patterns in chacma baboons (*Papio ursinus*) across southern Africa

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Abstract

Animals need to adjust their diel activity patterns to fulfil their energy and social requirements whilst avoiding predation risk and environmental constraints. The chacma baboon (*Papio ursinus*) is a highly adjustable primate occupying a variety of habitats in southern Africa, yet little is known about its diel activity patterns in different environments. We used camera trap data collected from 2016 to 2022 in 29 sites in South Africa and Zimbabwe to characterise the diel activity pattern variations of chacma baboons in different biomes (savanna, nama-karoo, fynbos, forest, thicket and grassland). We quantified activity using non-parametric kernel density functions and extracted activity level estimates, times of wake up, sleep and activity peaks. Chacma baboons' activity levels significantly decrease by approximately 2.84% with a unit increase in latitude. We did not find any significant effect of latitude on "wake up" and "go to sleep" time of chacma baboons. Within a day, chacma baboons are more active in the morning and the afternoon and their diel activity levels decreased with temperature, and precipitation throughout the day, but increased with predator activity at night and morning. The results show that chacma baboons can flexibly adjust to local conditions in rapidly changing southern African environments.

Keywords: activity patterns, latitudinal gradient, circadian rhythm, temperature, NDVI, predator avoidance.

Introduction

Wildlife's activity patterns, referring to the timing and vigour of animal activity throughout a 24-hour cycle, vary latitudinally among and within species (1,2) and are shaped by factors, including circadian rhythms (3,4), environmental conditions(5,6), and species-specific interactions (7,8). Although activity throughout the year is shaped by large-scale phenomena, like the spatio-temporal accessibility of food resources (9) or the search for reproductive opportunities (10), daily activity is fine-tuned to meet energy requirements (3), avoid heat stress (10), actual (7) or perceived (11) risk of predation, and mitigate competition (12). Diurnal activity offers advantages like predator detectability, thermoregulation and habitat exploration, while nocturnal activity provides benefits such as cooler temperatures and less competition (13). Carnivorous mammals have often evolved nocturnal habits, likely because of the benefits of reduced competition and increased stealth when hunting under the cover of darkness (14). In contrast, herbivorous mammals often exhibit diurnal activity patterns (13), which may be advantageous for locating plant resources during daylight, while reducing the risk of predation (13). This divergence in activity patterns underscores the complex interplay between ecological pressures, evolutionary strategies, and phenotypic adjustments (14).

Among non-human primates (NHPs), most anthropoid species (e.g. chimpanzees) are diurnal, with the exception of the nocturnal owl monkey, which shares a temporal niche with prosimian primates such as lemurs, lorises, and tarsiers (15,16). NHPs can adjust their activity patterns in response to environmental factors such as temperature (17,18), day length (19), resource availability (20), and predation (21,22). For example, the cathemeral mongoose lemur becomes more diurnal in the wet season and more nocturnal in the dry season to manage temperature and predation risk (20), while owl monkeys in Argentinean Chaco shift between nocturnal and diurnal activity based on seasonal conditions (24). The activity patterns of different NHP species have been shown to vary with predator-prey interactions (21,22), time budgets (23), and seasonal variations in food availability or specific environmental parameters (e.g. temperature or lunar cycles, (17)). However, most studies focus on specific populations at a single location. As a result, comparable information on populations from the same species across environmental gradients is lacking. A particularly interesting model for studying daily activity patterns across multiple biomes is the chacma baboon (*P. ursinus*).

The chacma baboon is sexually dimorphic, ecologically adaptable, and omnivorous species is the largest baboon species (24), and one of the most widespread non-human primates, ranging across much of southern Africa (25,26) (Figure 1). They commonly occur in savannahs

and grasslands, leveraging these open spaces for foraging and social activities, and inhabit forests, known for their abundant resources such as fruits, leaves, and insects (25). Remarkably, their adaptability extends to surviving in extreme environments like deserts, semi-deserts, and high-altitude mountainous regions (25,26). However, their range may shrink due to climate change (26), raising questions about their flexibility and adaptation strategies. Chacma baboons optimise their active hours, balancing foraging, resting, grooming, and socializing, while avoiding predation, heat stress, and energy deficiency (27,28). They adjust their activity patterns based on environmental conditions, shifting their activities to more favourable hours of the day (29). For instance, Ayers *et al*., (2020) using radio telemetry found evidence of nocturnal activity in chacma baboons inhabiting the western Soutpansberg Mountains, South Africa, as a response to seasonal fluctuations in day length and lunar luminosity. In another study, baboons at DeHoop Nature Reserve, South Africa, displayed mid-day resting and shade-seeking behaviours on hot days as a thermoregulatory mechanism (30). During dry summers, chacma baboons increase daily activity to compensate for declining food quality and availability (27,31). Predators such as lions (*Panthera leo*), leopards (*Panthera pardus*), and spotted hyenas (*Crocuta crocuta*), which are among the leading causes of non-anthropogenic adult baboon mortality (32,33), also influence baboon spatio-temporal habitat use, such as delaying morning activity to avoid leopards (34). Despite these adaptations, the drivers of variations in chacma baboon diel activity patterns across their geographic distribution remain poorly understood.

Historically, data on chacma baboons' daily activities were collected through direct observations of small, habituated troops and/or in captivity (27,35–37), but this approach faced challenges such as inadequate visibility and observer effects that could unintentionally alter activity patterns (38). Radio or satellite telemetry (GPS collars) provide indirect assessments of activity patterns (28,39,40), but it is costly and logistical complex to implement at multiple locations simultaneously. Consequently, non-invasive camera-trap monitoring has become increasingly popular for collecting data on diel activity patterns. Camera traps, which capture time-stamped images when animals are active, offer a systematic and effective method for estimating circadian rhythms and activity levels in baboon populations (40,43–47).

We analysed camera trap data from 29 study sites across six biomes (savanna, nama-karoo, fynbos, forest, thicket, and grassland) in South Africa and Zimbabwe, covering a latitudinal gradient ranging from 34.46° to 17.70° S. We analysed the diel activity patterns of chacma baboons in relation to latitude, abiotic factors (i.e. temperature, precipitation, food availability (Normalised Difference Vegetation Index (NDVI)), and biotic factors (i.e. diel

activity patterns of lions, leopards, and spotted hyenas). We hypothesised that: H1) Diel activity patterns vary with latitude, with baboons in southern regions, where conditions are more stable, being more active than those in the north; H2) In warmer environments, baboons are more active during cooler morning and evening hours to avoid heat stress, while those in cooler environments remain active throughout the day; H3) In areas with abundant food resources, baboons are less active than in areas with food scarcity, reducing energy loss due to less travel; H4) In locations with predators, baboons avoid predation by being more diurnal, reducing activity during dawn, dusk, and night when predators are most active (50,51).

Materials and method

Study areas and sites

Chacma baboons boast an expansive geographic presence across southern Africa, encompassing countries such as South Africa, Namibia, Botswana, Zimbabwe, Mozambique, Zambia, and Angola (Figure 1). In South Africa, chacma baboons are notably abundant, occupying diverse regions like the savannahs of Kruger National Park, the lush coastal forests along the Garden Route, the rugged terrains of the Drakensberg mountains, and even the semi-desert areas in the Western and Northern Cape (40,41). Similarly, in Zimbabwe, they occur across a wide breadth of habitats, from the savannahs of Hwange National Park to the mountainous landscapes of the Eastern Highlands (36). Here, we capitalised on existing camera trap data gathered across multiple biomes in South Africa and Zimbabwe, resulting in a dataset collected from 29 study sites, encompassing six distinct biomes (Figure 1). Most of the sites (n=19) were located within the savanna biome, with the remaining sites distributed across nama-karoo (n=4), fynbos (n=3), forest (n=1), grassland (n=1), and thicket (n=1) biomes (Supplementary Table 1; Figure 1).

Data collection

Camera trap data

In this study, we capitalized on pre-existing camera-trap sets deployed in Southern African regions for three projects, each with distinct objectives: Snapshot Safari, Panthera, and Cape Leopard Trust (42–44). Snapshot Safari is dedicated to the comprehensive monitoring of wildlife across varied African ecosystems and provides extensive datasets for research (42). Panthera's Southern Africa leopard monitoring program utilises camera trapping to provide data on leopard population trends (43). Finally, Cape Leopard Trust's camera trap initiative is dedicated to the study and preservation of the cape leopards (*Panthera pardus*) and other

wildlife within the Western, Northern and Eastern Cape provinces of South Africa (44). The primary objectives of these projects include gathering comprehensive data on animal presence, behaviour, and population dynamics. These data are instrumental in informing conservation efforts (42), addressing human-wildlife conflicts (45), conducting ecological studies (44,46), and facilitating biodiversity monitoring initiatives (47). For the Snapshot Safari project, infrared motion and heat-sensor cameras were systematically deployed following a standardised grid (for more details, refer to (42)). Each capture event consisted of a maximum of three images taken within five seconds of the trigger during daylight hours and one single image if the camera trap was triggered at night (42). Camera trap images were then meticulously classified and manually curated using both citizen science (Zooniverse; https://www.zooniverse.org) and trained laboratory assistance using Traptagger (TrapTagger; https://wildeyeconservation.org/trap-tagger-about/). In the case of the Cape Leopard Trust and Panthera projects, paired cameras were positioned facing each other at each station. Cape Leopard Trust cameras were set to take a burst of 3 images per trigger during the day, and 1 image by night. For the purpose of the current study, in the case were the animal was detected by both cameras, records from only one camera were retained for each station to avoid duplicates in areas with high animal detectability, such as roads, drainage lines, and animal paths (44,47). The Cape Leopard Trust data was classified using WildID (https://www.wildid.app/), a machine learning program that automatically identifies and labels animal species from images, and then user verified after classification. Photos from the Panthera surveys were classified by species through a combination of research team members and a machine learning algorithm, using Panthera's Integrated Data Software, PantheraIDS, a custom-built camera trap data processing package, within the R Statistical Environment (R Core Team, 2020).

Depending on the site, cameras were active between 2016 and 2022, with an average of 40 (minimum=9; maximum=77) camera stations per site (Supplementary Table 1). Monitoring efforts spanned a median of 349 (minimum=124, maximum=1,681) trap days per site (Supplementary Table 1). From this dataset, we extracted images of chacma baboons and of their primary predators, namely lions, leopards, and spotted hyenas.

Abiotic variables

To understand the ecological and environmental drivers influencing chacma baboon's diel activity patterns, we focused on three primary abiotic variables: (i) temperature, which is linked to heat stress, metabolic rates, and energy expenditure in animals (2,48); (ii)

precipitation, which impacts water availability, habitat quality, and resource availability and distribution(28,49); (iii) and NDVI, which is a proxy of primary productivity and food resource availability and habitat suitability (50,51). We extracted the average NDVI at the study site scale for 16-day periods from MODI13Q1.061 Terra Vegetation Indices 16_Day Global 250m dataset (*https://lpdaac.usgs.gov*) using Google Earth Engine (https://earthengine.google.com). Mean monthly rainfall was obtained from TerraClimate Monthly Climate and Climatic Water Balance for Global Terrestrial Surfaces dataset (52), and mean hourly temperatures were extracted from Era5-Land Hourly-ECMWF Climate Reanalysis dataset (53). We calculated the mean seasonal hourly temperature, mean seasonal NDVI, and mean seasonal rainfall for each study site, using a 500m radius buffer from the outermost camera trap stations positioned in each site.

Camera trap dataset merging and filtration steps

A total of 1,771,424 camera trap images containing mammal and bird species (Supplementary Figure 1) were obtained from all 29 surveys. This dataset was cleaned and filtered to remove duplicate records, correct date and time and exclude records with inconsistent date-time stamps (Supplementary Figure 1). Since recommended sample sizes for diel activity patterns are between 100 (54) and 500 observations (55), we selected sites where at least 200 chacma baboon capture events were obtained and ended up with a final dataset comprising 29 out of 61 considered sites (Figure 1, Supplementary Table 1). This process resulted in a refined dataset of 1,460,847 capture events, of which 268,121 were baboons, 11,849 were leopards, 8,999 were lions and 15,200 were spotted hyenas (Supplementary Figure 1). Only sites with at least 100 capture events of a certain predator were considered for the analyses of the effect of this predator on chacma baboon activity (n=25) (Lashley *et al.*, 2018).

Chacma baboon diel activity patterns modelling

Activity was defined as any instance when at least one individual was captured by a camera trap. The time of the first image in each capture event was used, and to account for latitude and seasonal variations in sunrise and sunset, capture times were converted to solar time using the 'solartime' function in the R package 'activity' (64). This ensured consistent day length across sites, ranging from 9.8 to 14.5 hours (Figure 1). Following recommendations of Peral, Landman and Kerley, (2022), no temporal independence filters were applied, ensuring that the full temporal resolution of the data was preserved for a more accurate analysis of activity patterns.

To characterise diel activity patterns in each studied site, non-parametric kernel density functions were applied using the 'fitact' function from the R package 'activity' (56), estimating activity levels as the proportion of time baboons were active during a 24-hour period, with $\boldsymbol{Activity\ level = 2\pi fmax}$, where $\boldsymbol{2\pi}$ represents time in radians and $\boldsymbol{fmax}$ is the maximum of the kernel density plot of chacma baboons per site. We assessed diel activity distributions of chacma baboons at each site using the 'densityPlot' function from the R package 'overlap' (57). The diel activity distribution, hereafter referred to as the 'activity distribution', describes the shape and pattern of the kernel density distribution curve over 24 hours.

To further analyse chacma baboons' diel activity patterns, six parameters were extracted: activity level estimate, activity distribution, time and height of maximum peak of activity, wake up and sleeping time. Using the 'findpeaks' function from the R package 'pracma' (66), we identified the timing and amplitude of activity peaks. "Wake-up" time was defined as the first inflection point, and "sleeping time" as the last deflection point, determined by calculating the first and second derivatives of the kernel density curve.

Since chacma baboon's diel activity patterns vary with seasons (58,59), capture events were separated between four seasons: autumn (March-May), winter (June-August), spring (September-November) and summer (December-February), and activity level estimates in each season within each site were extracted by replotting the kernel density functions in R package 'activity'.

To refine activity level estimates throughout the day, we divided the day into six periods: (i) dawn (one hour before sunrise to sunrise), (ii) morning (sunrise to noon), (iii) midday (noon to two hours after noon), (iv) afternoon (the remaining time between mid-day and dusk) (v) dusk (sunset to one hour after sunset), and (vi) night (one hour after sunset to one hour before sunrise) (7,60). For each capture event, sunrise, noon and sunset times were determined using geographical location and date of the capture event, employing the function 'getSunlightTimes' from R package 'suncalc' (61). Noon was defined as the time when the sun reaches its highest point in the sky (local celestial meridian). To obtain fractions of activity level estimates per each day period in each season across sites, we used the function 'integral' in R package 'pracma', which computes the numerical integration $\int_{\boldsymbol{b}}^{\boldsymbol{a}} \boldsymbol{f(t)dt}$ where $\boldsymbol{f(t)}$ is the activity kernel density function and $\boldsymbol{a - b}$ is the corresponding time interval for each day period.

Statistical analysis

Chacma baboon's diel activity patterns.

To characterise and determine whether the activity patterns of chacma baboons varied with the geographical location, we analysed the effect of latitude on five of the six parameters extracted (activity level estimate, time and height of the maximum activity peak, wake-up time, and sleeping time) using beta regression for activity level estimate and linear regression models for the rest. We checked the preliminary assumptions of normal distribution and homoscedasticity of the residuals of the models using the function 'simulateResiduals' in the R package 'DHARMa' (62). We used beta regression models (R package 'glmmTMB', (63)) to determine if the total activity level estimate varied with latitude. We also investigated seasonal differences (summer, autumn, winter, and spring) in activity level estimates using a Kruskal-Wallis' test. Finally, we tested for differences in activity level estimates among sites within each day period (dawn, morning, mid-day, afternoon, dusk, and night) using a Kruskal-Wallis' test. We did not include comparisons of activity patterns among biomes due to the uneven distribution of sampled sites across biomes (Range=1-19 sites, Figure 1).

Variables influencing chacma baboon's diel activities

Firstly, we tested the additive effect of three abiotic factors (temperature, precipitation and NDVI) on the activity level estimates of chacma baboons using Beta regression models ('glmmTMB' R package; (63)). We checked the preliminary assumptions of beta distribution and homoscedasticity of the residuals of the model using the function 'simulateResiduals' in the R package 'DHARMa' (62). We checked the absence of multicollinearity among the explanatory variables by the variance inflation factor (VIF) using the 'check_collinearity' function in the R package 'performance' (64). The best model was selected for interpretation after removing outliers for all periods of the day except for dawn and night (a maximum of 2 outliers were removed). To ensure comparison, all explanatory variables were standardised by subtracting their mean and dividing by the global standard deviation.

Secondly, we tested the additive effect of predators' activity level estimates on chacma baboons' activity level estimates. Our analysis focused on sites where at least one of these predator species (lion, leopard, spotted hyena) was detected. We applied the same methodology used for baboons to calculate activity level estimates for these predators at the selected sites and day periods. Separate Beta regression models were then run for each predator species to assess how their activity during specific periods and seasons influenced baboon activity, while considering the previously described abiotic covariates as additive effects. Model assumptions and multicollinearity were checked as described above.

Finally, we quantified the temporal tolerance and avoidance of chacma baboons toward predators by examining the overlap coefficients, a unitless value ranging from 0 (no overlap) to 1 (complete overlap). To compare the probability density functions between chacma baboons and each predator species in each site, and test if they arise from the same distribution (i.e. are characterised by a significant overlap), we used the function 'CompareCkern' in the R package 'activity' (56). We used bootstrapping (n=500 iterations) to obtain 95% confidence intervals (65). We plotted the activity curves for chacma baboons and each predator across all sites using the 'densityPlot' function in the 'overlap' R package (57) (Supplementary Figure 3). All statistical analysis were done in R software version 4.3.1 (R Core Team, 2023).

Results

Differential diel activity patterns across Southern African biomes

Our results revealed that, while chacma baboons in the southern sites appeared to “wake up” and “go to sleep” earlier than those in the northern sites (as indicated by numerical differences in Figure 2C and 2D respectively), no significant differences were observed with increasing latitude (wake up time: β=-0.01, p=0.77, Figure 2C; sleeping time: β=-0.03, p=0.4, Figure 2D).

Among the 29 sites analysed, chacma baboons displayed the highest total activity level estimate in the southern site, Garden Route National Park (0.44 ±0.01, forest biome), and the lowest total activity level estimate in one of the northern sites, Venetia (0.15 ±0.005, savanna biome) (Figure1, Figure 2A). The height of chacma baboon's maximum peaks of activity varied among sites within biomes (Figure 1, Supplementary Figure 2). Chacma baboons exhibited higher total activity level estimates in the southern than in the northern regions (Figure 2A). The total activity level estimates of chacma baboons significantly decreased by 2.84% per unit movement from south to north units (β=0.028 ±0.01, *p*-value=0.02).

Baboons living in 9 of the 19 savanna sites, as well as in the Garden Route National Park (forest biome), showed a trimodal activity distribution, with the maximum peak of activity in the morning (between 0530 hrs and 1127 hrs) for most savanna sites and at dusk (1815 hrs) for the forest site. In Tswalu Kalahari Game Reserve, Madikwe National Park and Associate Nature Reserves (semi-arid extreme of the savanna biome), baboons displayed a unimodal distribution, with the maximum peaks of activity occurring in the afternoon (1428 hrs), mid-day (1303 hrs) and morning (0931 hrs) time periods, respectively. A unimodal activity pattern was also observed in all sites located in the nama-karoo. and in De Hoop Nature Reserve (fynbos biome), with baboons displaying their main activity peak during mid-day (mean=1159

hrs; Figure 1, Supplementary Figure 2). A distinctive bimodal activity pattern was observed in iThala Game Reserve (maximum activity peak at 0820 hrs, grassland biome) and Zingela Nature Reserve (maximum activity peak at 1718 hrs, thicket biome; Figure1). In the fynbos biome, chacma baboons' activity was multimodal, with the maximum peak of activity at 1124 hrs in Overberg (fynbos biome) and 1539 hrs in Little Karoo (Figure 1). Linear regression models showed that the height of the maximum peak of activity significantly increased with latitude (β=0.004, p=0.03, Figure 2B), showing that northern sites had higher maximum activity peaks than southern sites.

Chacma baboons are more active in the mornings and afternoons

Our analysis revealed that chacma baboons' activity level estimates vary among day periods (dawn, morning, mid-day, afternoon, dusk, and night) within a 24-hour day cycle. We found that chacma baboons were most active (52.5% of all detections and showed the most across sites variation (range=8-84% of total per site activity level estimates; Figure 3) in the morning, and then during the afternoon (20.8% of all detections), followed by mid-day (17.6% of all observations), dawn (5.8%), night (2.9%) and eventually dusk (0.3% of all detections; Figure 3).

Chacma baboon activity level estimates significantly varied among sites across almost every period of the day, namely dawn, morning, mid-day and night (Table 1). In the afternoon this variation was only marginally non-significant (Table 1). No chacma baboons' activity was detected at night in Samara, De Hoop, Chirisa, Chizarira and Associate Private Nature Reserves. Similarly, there were no chacma baboon detections in De Hoop, Chizarira and Samara at dawn, and in more than half of the savanna sites at dusk.

Abiotic factors on the timing of chacma baboon's activity

Results from our beta regression models, the observed per-site variations in diel activity level estimates of chacma baboons within each day period were primarily explained by variations in temperature (Figure 4A). Chacma baboons consistently showed lower activity levels in sites with higher temperatures throughout the day, although the effect was not significant during the morning (p=0.96; Figure 4.A) and at dawn (p=0.09; Figure 4.A). Additionally, precipitation emerged as a significant factor reducing activity level estimates at dawn ($p<0.001$) and at night (p=0.008; Figure 4.A). Finally, NDVI had a significant negative effect on activity level estimates only at mid-day (p=0.006; Figure 4.A), with no notable impact observed during other periods of the day.

Predators

All tested predators had a positive effect on chacma baboons' activity level estimates at night (lions: β=0.21±0.08, p=0.01; leopards: β=0.20±0.09, p=0.03; spotted hyenas: β=0.16±0.07; p=0.06; Figure 4B). Similarly, leopards showed a significant positive effect on chacma baboons' activity level estimates in the morning (β=0.2±0.1, p=0.05; Figure 4B). Conversely, leopards had an almost significant negative effect on baboon activity at dawn (β=-1.7±0.9, p=0.06; Figure 4B). These predator effects were not significant during most periods of the day, apart from morning and night (Figure 4B).

Chacma baboons and predator activities overlapped to varying degrees across different sites (spotted hyena: range=0.05-0.3; leopard: range=0.14-0.55; lion: range=0.07-0.65; Figure 5). The lowest overlap was observed between chacma baboons and spotted hyenas (Dhat4 > 0.31±0.09 for all sites; Figure 5). We observed a moderately lower overlap between chacma baboons and leopards (Dhat4 ranging from 0.31±0.01 to 0.55±0.01 in 16 out of 20 sites; Figure 5). In contrast, lions and chacma baboons showed a moderately high overlap (Dhat4 > 0.52±0.01 in one-third of the sites; Figure 5).

Discussion

Time plays a vital role in ecological and evolutionary responses. Our main objective was to determine whether chacma baboon diel activity patterns varied across a latitudinal gradient and analyse whether these variations were driven by abiotic factors and/or predators. While other studies have reported site-specific temporal variability in baboon activity (28,30), this study is the first to quantify diel activity patterns on a larger spatio-temporal scale. Using seven years of camera traps data from 29 sites across 6 southern African biomes, we revealed landscape-level variation in chacma baboon activity patterns (Figure 1) and to identify the key drivers of these variations.

Consistent with our *geographical perspective* hypothesis (H1), we showed that chacma baboons activity levels decreased along a north-south gradient, with the highest level in the southernmost Garden Route National Park (Figure 2A). This may reflect and ecological or evolutionary response to varying environmental conditions along the latitudinal gradient (66). Latitude influences multiple biological parameters (e.g. temperature, precipitation etc.), that are more stable in southern sub-Saharan Africa and more seasonal further north (67). Stable environmental conditions in southern sites support resources stability, reducing the trade-offs between resource acquisition and environmental adversary by chacma baboons, hence high

activity levels. These latitudinal variations reflect the chacma baboons' adaptability to environmental challenges and the significant role of latitudes in shaping their behaviour.

After correcting for differences in day length across latitudes, results showed that chacma baboons in the southern sites wake up (Figure 2C) and go to sleeping sites (Figure 2D) at the same time as those in the northern sites. This suggests baboons synchronize their diel activity patterns with the local circadian rhythm, regardless of latitude or environmental variations. This synchronisation likely stems from changes in light at dawn and dusk time, which reset the circadian rhythm (68). Therefore, adjusting for daylength variations using sunrise and sunset times as zeitgebers, eliminated most of the differences. Similar relationships between wake-up and sleeping times and sunrise/sunset have been observed in chacma baboons (69) and other non-human primates (70), though Davidge showed that baboons in Cape Peninsula in South Africa began activity independently of sunrise time (27). This suggests some flexibility in the baboons' circadian rhythm, allowing them to adapt to local conditions while maintaining stable daily activity pattern across different geographical locations.

Although we observed some evidence of nocturnal behaviour, chacma baboons were predominantly diurnal, with most activity occurring in the morning and afternoon at all sites. This diurnal behaviour has been already reported for chacma baboons, in Soutpansberg Mountains, South Africa (28) and Cape Peninsula (27,37,69). Nocturnal activity observed in our study may be a compensatory mechanism to recover for resting time loss during hot days, or it could be triggered by disturbances at sleeping sites, such as predators' presence (71). Our analysis suggests that multiple environmental factors influence simultaneously the diel activity patterns of chacma baboons through the day.

Partially contrasting with our *thermoregulatory perspective* hypothesis (H2), we found variation chacma baboon activity patterns across biomes: unimodal in semi-arid savanna and hot and dry nama-karoo sites, bimodal in grasslands and thicket biomes and multimodal in savanna and forest sites (Figure1). These patterns reflect a complex interplay between energy requirements, thermoregulatory needs and predation risks. In semi-arid savannas and nama-karoo biomes, where temperatures are high and productivity is low (72), chacma baboons maximise activity through the day to meet energy needs, unlike those in more productive biomes like forests, where they rest more frequently. This contrasts with the bimodal patterns found in grasslands and thickets, where baboons avoid heat stress by being more active in the cooler morning and late afternoon hours, similar to other primates like *Propithecus v. verreauxi* (20), *Eulemur mongoz* (19) in Madagascar, *Aotus a. azarai* in Argentinean Chaco (70), as well as other mammals like *Syncerus caffer* in South Africa (73), and *Oryx leucoryx* in Mahazat as-

Sayd, in Sudi Arabia (Hetem *et al.*, 2014). In line with Stelzner's study on Amboseli yellow baboons (*Papio cynocephalus*), baboons in arid regions may trade off thermoregulation for feeding during times of limited food availability (74). In contrast, Hill observed that chacma baboons at De Hoop in the fynbos site increased resting time and reduced activities in response to high temperatures, thank to more diverse seasonal resources (30).

Partially consistent with our *thermoregulatory perspective* hypothesis (H2), temperature appears to a key driver of activity, with lower activity level estimates in sites with consistently high temperatures (Figure 4A). This suggests thermoregulatory constraints significant shape how chacma baboons use their time, reducing activity during the cooler parts of the day to conserve energy and avoiding heat stress during the hotter midday and afternoon periods. These findings are consistent with previous studies showing baboons engage in less energy-demanding activities in high temperatures and seek shade (59,74), similar to *Macaca sylvanus* in Algeria and Morocco (17). In contrast, chacma baboons in colder mountains (such as those at the Lajuma Research Centre in South Africa) adjust their activity by being active in the warmer hours of the day (17), with earlier wake-up times in summer season compared to cooler winter season (28).

Supporting our *food availability* hypothesis (H3), we found a strong negative correlation between precipitation and baboon's activity at dawn and night (Figure 4A), suggesting that chacma baboons in low rainfall areas extend activity during these times to meet energy requirements. Additionally, baboons reduced mid-day activity in response to higher NDVI, aligning with the fact that precipitation and NDVI are indicators of seasonal food availability in southern African biomes (49,51). This is consistent with a time budget analysis in Cape Peninsula, South Africa, which found reduced foraging and movement time during seasons of high food availability (31). While NDVI significantly influenced mid-day activity, this suggests that food availability's impact is more pronounced during that time.

We did not observe significant seasonal differences in chacma baboon activity levels, likely because many seasonal variations are tied to changes in day length across seasons. By correcting for this, much of the variation was removed (75). For instance, previous studies have shown baboons in Cape Peninsula are more active during long summer days compared to short winter days (31). The wide latitudinal gradient in our study area adds further complexity, with southern biomes experiencing wet and cold winters, and northern regions having dry, cold winters, making consistent seasonal trends harder to detect. Similarly, Hill and others found that day length was the main factor influencing baboons activity at De Hoop Nature Reserve (59).

The positive relationship between chacma baboons' nighttime activity and the presence of their main predators (lion, leopard, and spotted hyena) contrasts with our initial predictions of temporal avoidance based on the predation hypothesis (H4) (Figure 4B). This unexpected result may be explained by increased mobility due to agitation and mobbing behaviour as part of anti-predatory strategies, rather than avoidance (35,82). For example, baboons in Serengeti National Park have been observed mobbing and fleeing after predation events (83), though these behaviours typically occur during the day (34). This finding also highlights the role of thermoregulation and feeding, as baboons may trade off predation risk by co-occurring with predators during daylight hours. Predators like lions, leopards, and hyenas, which are often nocturnal or crepuscular, are less effective hunters in daylight (2,7,56). Although beta regression assumptions were not fully met for the model with morning activity, we found that leopard activity increased with that of chacma baboons (Figure 4B). Overlap coefficients between baboon and predator diel activities supported this, showing generally low overlap with leopards and hyenas, indicating distinct temporal niches (Figure 5). However, variations were noted, particularly in the overlap with lions, making clear conclusions difficult. Nevertheless, beta regression provided a more rigorous analysis, offering valuable insights into the temporal interactions between baboons and their predators.

Conclusion

Our findings reveal significant variations in diel activity patterns of chacma baboons across different latitudes, demonstrating their ability to adapt to food availability, temperature fluctuations and predation risk. This enhances our understanding of their ecology and temporal niche, fundamental information for predicting their future in the face of climate change.

In southern Africa, chacma baboons, like other wildlife, are threatened by habitat loss, agricultural expansion, and limited dispersal due to the coast. Their complex relationship with humans, often marked by competition for resources, has led to persistent conflicts (26,76). Integrating a deeper understanding of their cognitive behaviour (77), landscape of fear (78), and feeding requirements (79), in conjunction with their activity patterns can inform management decisions to help reduce these conflicts. Our study shows that baboons are most active between 0500 and 1800 hours, with morning peaks, suggesting that activities like waste disposal or food storage left unsecured during this time increase conflict risks. Implementing targeted baboon monitoring in these periods could reduce human-baboon interactions. Future research should explore how climate change may impact their diel activity patterns and

investigate the genetic basis of behavioural adaptations across populations, shedding light on the evolutionary mechanisms supporting their survival in changing environments

Authors' contributions

Locadia Dzingwena: Methodology, Data acquisition, Formal analysis, Investigation, Writing- Original Draft, Visualisation, Writing- Review & Editing. **Virginie Rougeron:** Conceptualization, Methodology, Data acquisition, Investigation, Writing- Review & Editing, Supervision, Funding acquisition, Visualisation. **Franck Prugnolle:** Methodology Writing- Review & Editing, Supervision. **Lucie Thel:** Methodology, Writing- Review & Editing, Supervision. **Elise Huchard:** Methodology, Writing- Review & Editing, Supervision. **Herve Fritz:** Data curation, Writing- Review & Editing. **Jan Venter**: Data curation, Writing- Review & Editing. **Marc Choisy:** Methodology, Formal analysis, Writing- Review & Editing
Rebecca Garbet: Data curation, Writing- Review & Editing. **Anita Wilkinson:** Data curation, Writing- Review & Editing.

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Competing interests

The authors declare that they have no competing interests

Data availability statement

The data used in this study are available in supplementary material. The raw camera-trap data employed in this study can be requested at Snapshot Safari (snapshotsafari.org), Cape Leopard Trust (research@capeleopard.org.za) and Panthera (panthera.org).

Code availability

The code to analyse and reproduce this study is available in supplementary material.

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Table legends

Table 1: Difference in activity level estimates among sites in different periods of the day (Kruskal Wallis test).

Period of the day	Number of observations	Kruskal Wallis test statistic ($\chi 2$)	Degrees of freedom	p-value
Dawn	16514 (5.8%)	42.5	28	0.040
Morning	148282 (52.5%)	47.3	28	0.010
Mid-day	49822 (17.6%)	51.8	28	0.004
Afternoon	58844 (20.8%)	39.1	28	0.080
Dusk	974 (0.3%)	34.0	28	0.200
Night	8059 (2.9%)	42.6	28	0.040

Figure legends.

Figure 1. Examples of activity distributions of chacma baboons in different biomes and geographic distributions. The sources of camera trap data are indicated in white for Panthera, purple for Snapshot Safari and black for Cape Leopard Trust. The numbers on the map correspond to: 1. Venetia Limpopo Nature Reserve; 2. Lajuma Nature Reserve; 3. Welgevonden Game Reserve; 4. Timbavati Private Nature Reserve; 5. Makalali Game Reserve; 6. Lapalala Wilderness; 7. Associate Private Nature Reserves; 8. Pilanesberg National Park; 9. Madikwe Game Reserve; 10. Khamab Kalahari Reserve; 11. Tswalu Kalahari Reserve; 12. uMkhuze Game Reserve; 13. Phinda Private Game Reserve; 14. Manyoni Private Game Reserve; 15. Ithala Game Reserve; 16. Hluhluwe Game Reserve; 17. Eastern Shores; 18. Zingela Nature Reserve; 19-20. Samara Private Nature Reserve & De Nek Farm; 21. Mountain Zebra National Park; 22. Karoo National Park; 23. Overberg; 24. Little Karoo ; 25. Garden Route National Park; 26. DeHoop Nature Reserve; 27. Save Valley Conservancy; 28. Chirisa Safari Area; 29. Chizarira National Park. The Y-axis represents the density of activity, and the X-axis represents the hours throughout the day (in solar time, see text for details). Each day is divided into six periods: dawn and dusk (grey), morning and afternoon (yellow), mid-day (orange), and night (black).

Figure 2. Diel activity patterns of chacma baboons of the 29 study sites across a latitudinal gradient and six Southern African biomes: Fynbos (grey), Forest (black), Nama-karoo (light green), Thicket (pink), Grassland (light peach) and Savanna (green)**. A.** Total activity level estimates. **B.** Height of maximum peak of activity. **C.** Wake up time. **D.** Sleeping time. The dots correspond to the raw data, the solid line represents the predicted values from the best model, the shaded area represents the 95% confidence intervals estimated from the model.

Figure 3. Biome specific average diel activity level estimate of chacma baboons per day period (i.e. dawn, morning, mid-day, afternoon, dusk and night). Within each caption, light grey dots represent site-specific activity level estimates. The coloured dots indicate the average probability of activity within each biome: Fynbos (grey), Forest (black), Nama-karoo (light green), Thicket (pink), Grassland (light peach) and Savanna (green). Vertical lines depict the 95% confidence interval for the average activity level estimates for each biome. Wider confidence intervals indicate greater variation among sites within each biome.

Figure 4. Drivers of variation in the total activity level estimates of chacma baboons in each day period: A. Abiotic variables, namely temperature, precipitation and NDVI. **B.** Biotic variables, namely lion, leopard and spotted hyena total activity level estimates (whilst controlling for temperature, precipitation and NDVI). The blue dots indicate significant mean coefficient estimate and the grey dots indicate non-significant mean coefficient estimates of beta regression at **α=0.05.** The bars represent 95% confidence intervals. Note the change of Y-axis scale between A and B.

Figure 5. Overlap coefficient Dhat4 (see text) between chacma baboon and predator activity patterns in each site: spotted hyena (circles), leopard (triangles) and lion (squares).

Figure 1.

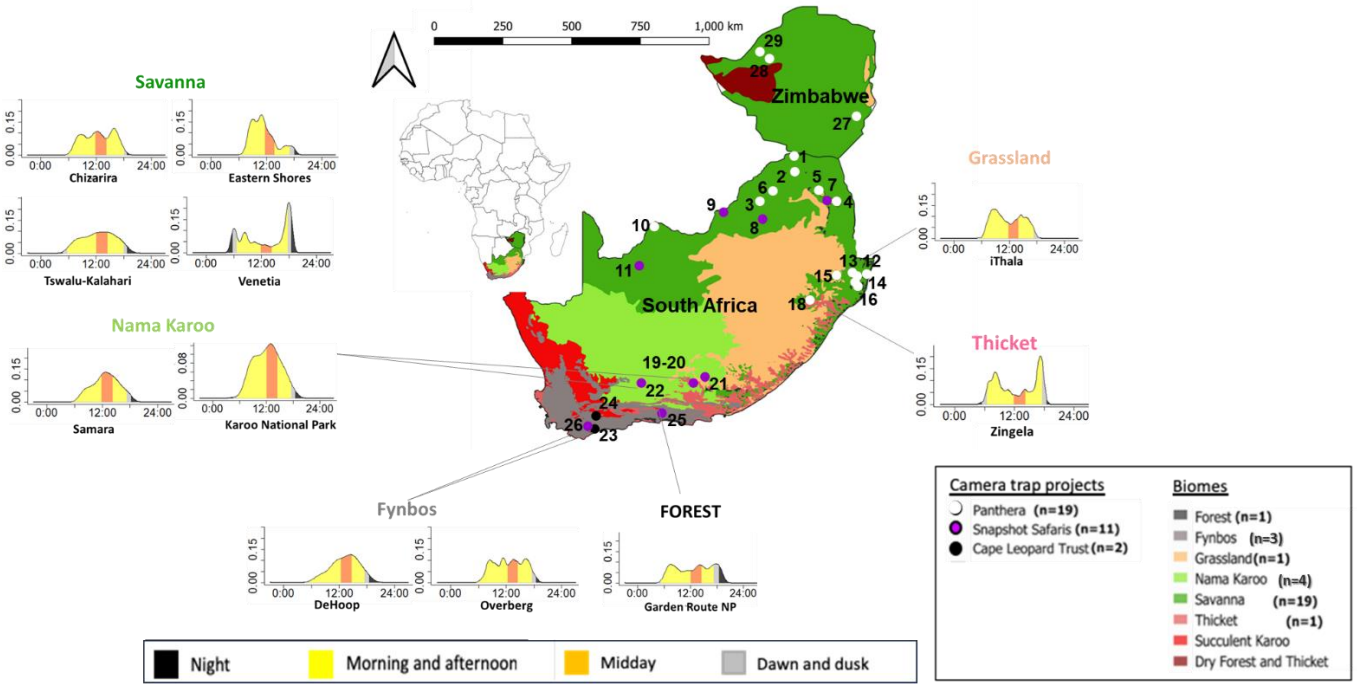

0 250 500 750 1,000 km
Zimbabwe
South Africa
Savanna
Chizarira
Eastern Shores
Tswalu-Kalahari
Venetia
Nama Karoo
Samara
Karoo National Park
Grassland
iThala
Thicket
Zingela
Fynbos
DeHoop
Overberg
FOREST
Garden Route NP
Night
Morning and afternoon
Midday
Dawn and dusk
Camera trap projects
Panthera (n=19)
Snapshot Safaris (n=11)
Cape Leopard Trust (n=2)
Biomes
Forest (n=1)
Fynbos (n=3)
Grassland(n=1)
Nama Karoo (n=4)
Savanna (n=19)
Thicket (n=1)
Succulent Karoo
Dry Forest and Thicket

Figure 2.

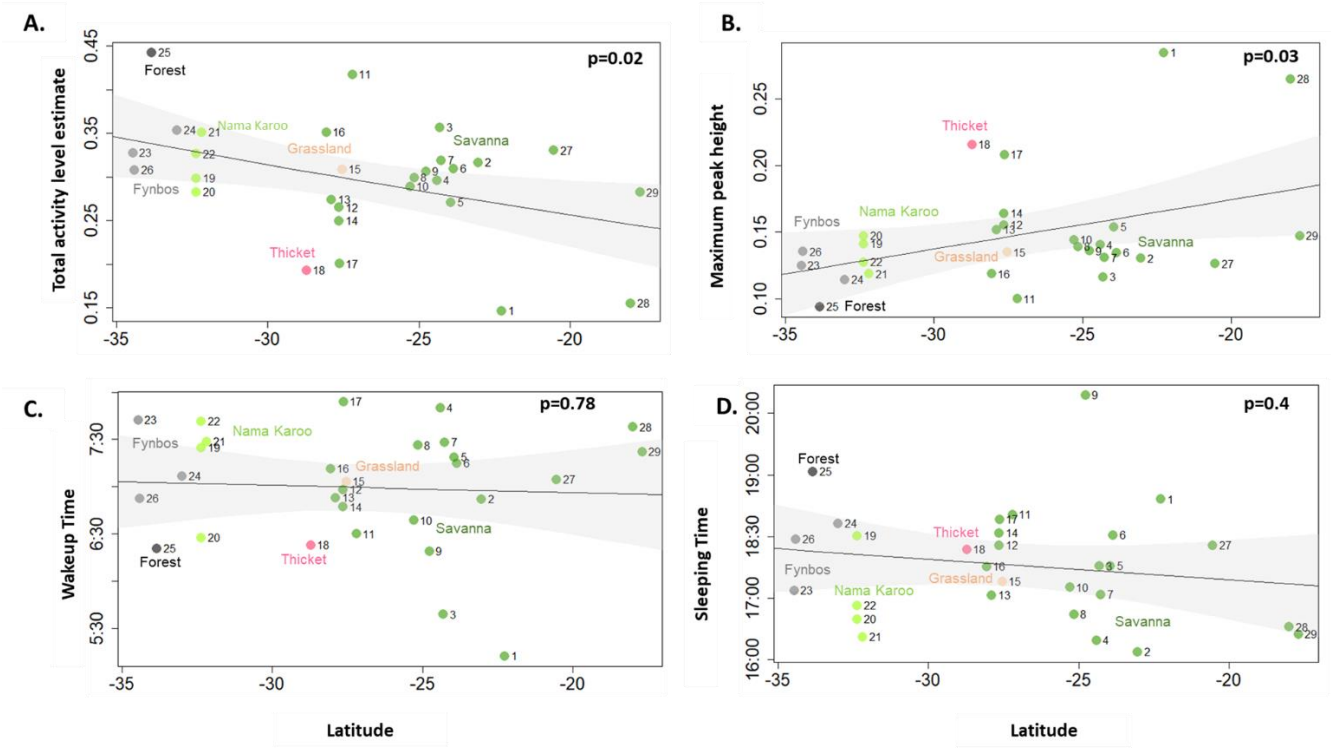

A.
p=0.02
Total activity level estimate
Forest
Nama Karoo
Grassland
Savanna
Fynbos
Thicket
B.
p=0.03
Maximum peak height
Thicket
Fynbos
Nama Karoo
Grassland
Savanna
Forest
C.
p=0.78
Wakeup Time
Fynbos
Nama Karoo
Grassland
Savanna
Forest
Thicket
D.
p=0.4
Sleeping Time
Forest
Thicket
Fynbos
Grassland
Nama Karoo
Savanna
Latitude
Latitude

Figure 3.

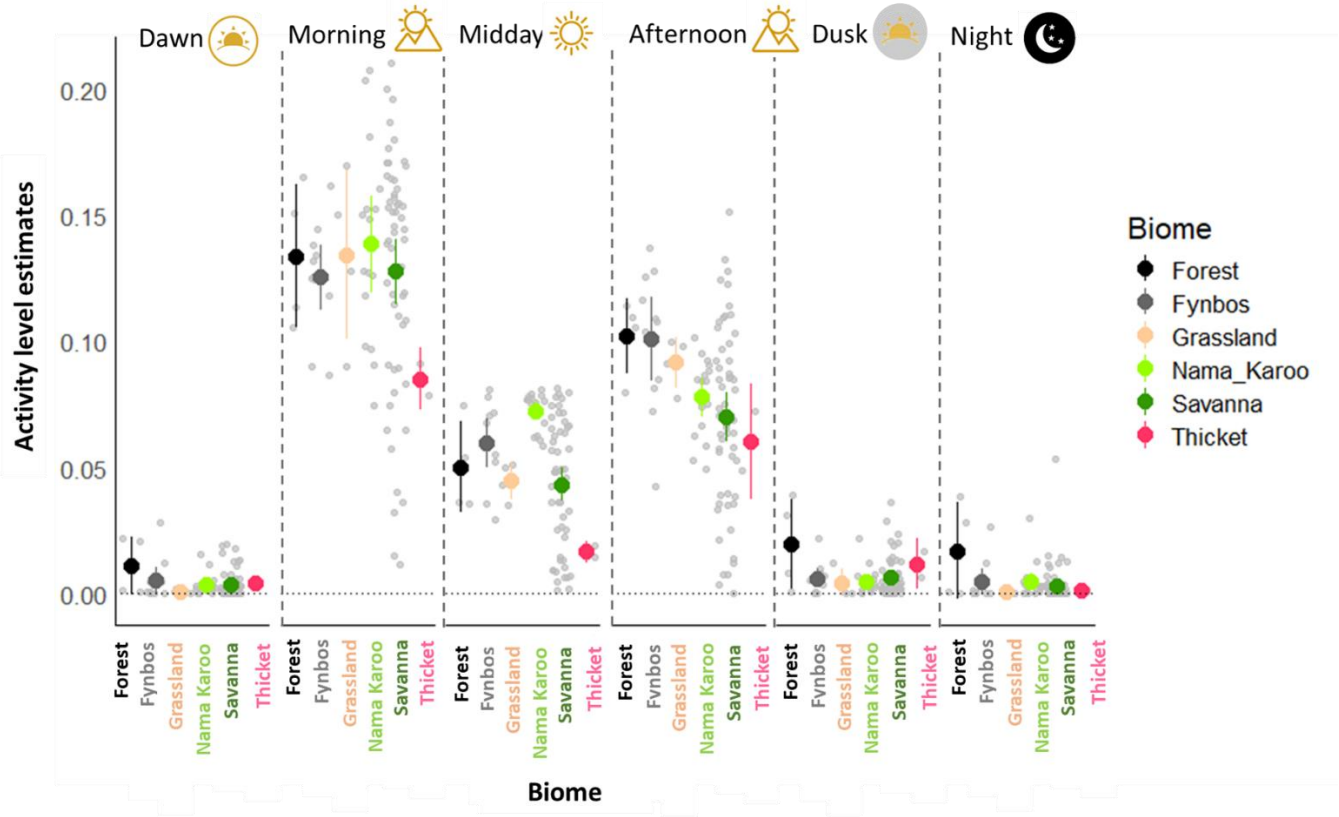

Dawn
Morning
Midday
Afternoon
Dusk
Night
Activity level estimates
0.20
0.15
0.10
0.05
0.00
Forest
Fynbos
Grassland
Nama Karoo
Savanna
Thicket
Biome
Biome
Forest
Fynbos
Grassland
Nama_Karoo
Savanna
Thicket

Figure 4.

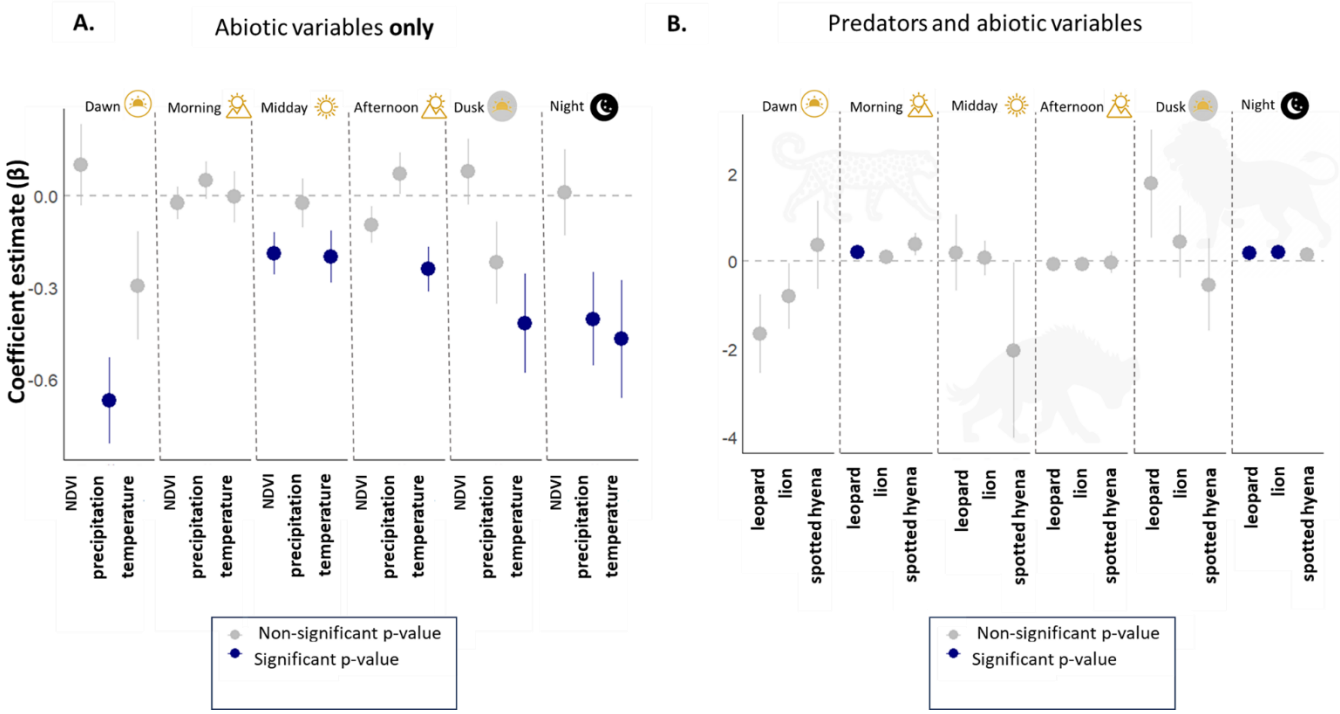
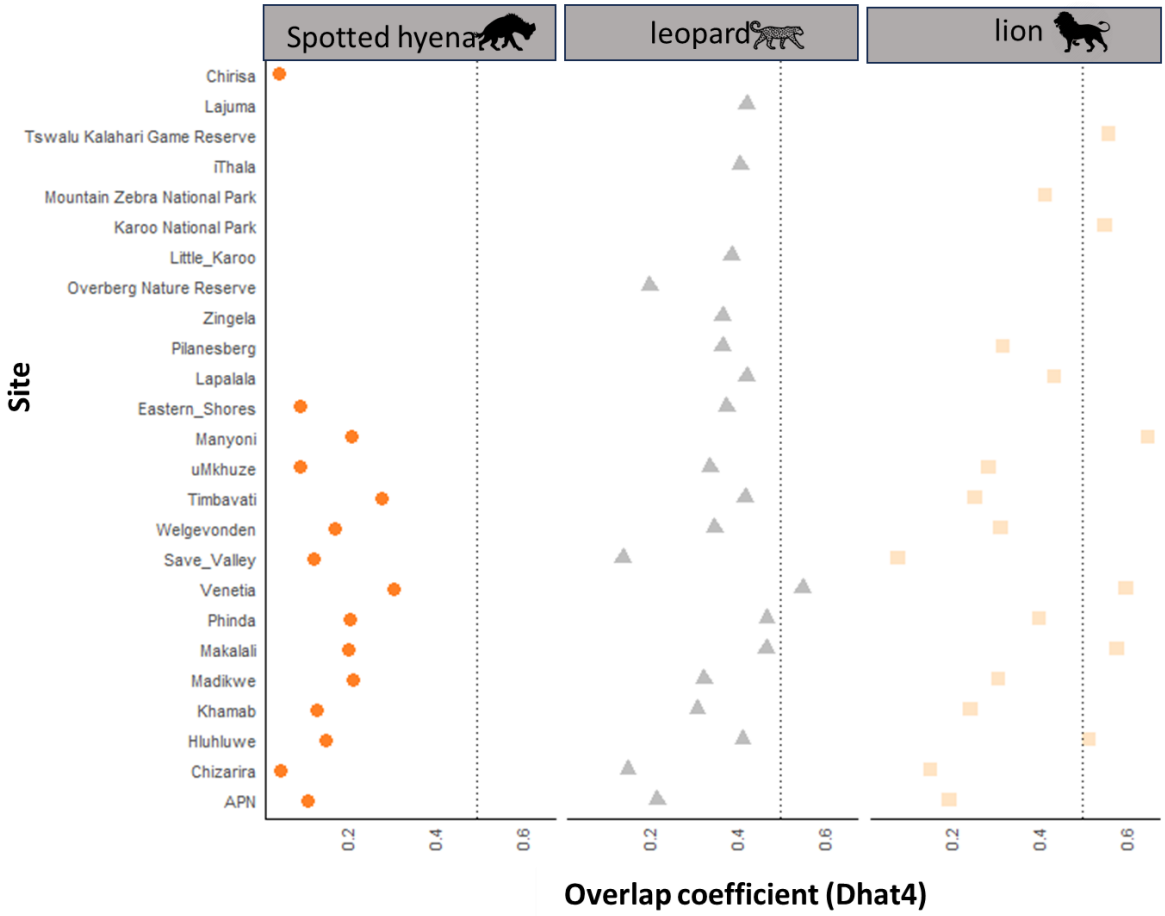

A.
Abiotic variables only
B.
Predators and abiotic variables
Dawn
Morning
Midday
Afternoon
Dusk
Night
Coefficient estimate (β)
0.0
-0.3
-0.6
2
0
-2
-4
NDVI
precipitation
temperature
leopard
lion
spotted hyena
Non-significant p-value
Significant p-value

Figure 5.


Spotted hyena
leopard
lion
Site
Chirisa
Lajuma
Tswalu Kalahari Game Reserve
iThala
Mountain Zebra National Park
Karoo National Park
Little_Karoo
Overberg Nature Reserve
Zingela
Pilanesberg
Lapalala
Eastern_Shores
Manyoni
uMkhuze
Timbavati
Welgevonden
Save_Valley
Venetia
Phinda
Makalali
Madikwe
Khamab
Hluhluwe
Chizarira
APN
0.2
0.4
0.6
Overlap coefficient (Dhat4)

806