

Research article

Tracking Enclosure Use in Mixed-Species Exhibits: Insights from the Zoo-Observer App

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Abstract

Understanding how zoo animals use their enclosures is essential for welfare-oriented management. This study demonstrates how digital tools like the Zoo-Observer app can enhance spatial behaviour monitoring by enabling the collection of fine-scale positional data, including home range estimates and walking distances. We applied this approach to Rothschild's giraffes *Giraffa camelopardalis rothschildi*, Grant's zebras *Equus quagga boehmi*, and blue wildebeests *Connochaetes taurinus taurinus* housed in a mixed-species savannah exhibit at Opel-Zoo, Germany. Data were collected over two consecutive years, enabling a unique comparison to be made of the behaviour of the same social groups before and after the birth of juveniles. The temporary relocation of hay feeding sites was used as a low-effort intervention to test behavioural flexibility. While zebras adjusted their enclosure use, giraffes and wildebeests remained spatially stable, reflecting their species-specific foraging strategies and social dynamics. Our findings demonstrate that combining behavioural observations with spatial metrics, such as covered distance, provides a more comprehensive understanding of enclosure use and activity patterns. This approach informs evidence-based, species-specific husbandry decisions and demonstrates the potential of app-based tools for monitoring.

Introduction

Managing animal care and behaviour in modern zoos presents multiple challenges. Balanced management should consider the behavioural needs of the animals, including opportunities for feeding, resting, and movement, while simultaneously fulfilling expectations of zoo staff and visitors. From the visitors' perspective, enclosures should resemble the animals' natural habitats (Fàbregas et al. 2012), but also ensure the visibility and activity of animals to maintain visitor interest and engagement (Margulis et al. 2003). Therefore, enclosure design can have a direct impact on both animal behaviour and the visitor experience (Finch et al. 2022). In addition to visibility and aesthetics, the way animals interact with different parts of their enclosure provides crucial insight into their welfare. The exhibition of a broad spectrum of species-typical behaviours is widely recognised as a positive welfare indicator (McPhee and Carlstead 2012). However, designing enclosures that meet these behavioural needs becomes particularly complex in mixed-species exhibits, where multiple species with different space requirements, social structures, and behaviours

cohabitate. For example, ensuring that all species have access to key resources, such as feeding stations and retreat areas, without creating conflict or stress, is a major goal of enclosure planning.

Understanding how certain species, or even individuals within species, use the enclosure is crucial for evaluating enclosure effectiveness and detecting potential welfare issues (Ross et al. 2009). If one species or individual monopolises a preferred feeding site or consistently avoids an area, this may reflect dominance relationships, spatial exclusion, or resource competition, all of which have implications for welfare and management. Additionally, repetitive locomotion in a restricted area might indicate boredom or stereotypy, suggesting a need for targeted enrichment or structural change (Mason 1991; Rose et al. 2017; Yasmeen et al. 2022). In zoological institutions, feeding site placement is one of the most influential and easily adjustable aspects of enclosure design (Puehringer-Sturmayer et al. 2023; Quintanilla et al. 2023; Bähler et al. 2024; Fens and Clauss 2024). It not only shapes feeding behaviour but also affects activity levels, space use, and social interactions among individuals and species (Quintanilla et al.

2023; Fens and Clauss 2024). Despite its central role in animal husbandry, few studies have systematically evaluated the impact of relocating feeding sites on animal behaviour and movement within mixed-species enclosures. Such changes could either promote more diverse enclosure use or, conversely, reinforce existing spatial or social patterns. Understanding species-specific responses to environmental modifications such as feed relocation is therefore essential for designing effective enrichment and space management strategies that support welfare and natural behaviours.

Historically, studies have often focused on activity budgets to assess enclosure use and natural behaviours of animals to evaluate their welfare in zoos (Andersen 1992; Veasey et al. 1996; Burger et al. 2020). However, more recent studies have emphasized the importance of concurrent collection of both spatial and behavioural data (Rose and Riley 2021; Güberr and Dierkes 2024; Zacchi et al. 2024). Combining spatial data (e.g., locations, paths, distances) with behavioural data (e.g., resting, feeding, locomotion) can yield valuable insights. For instance, it can reveal whether certain areas are avoided, whether interspecies interactions influence movement patterns, or whether repetitive use of specific routes indicates poor welfare (Scott et al. 2016; Whitham and Miller 2016). Long-term spatial and behavioural data allow for the detection of patterns and changes over time, which is especially relevant when changes occur in enclosure structure or group composition (Holdgate et al. 2016; Troxell-Smith et al. 2017; Brereton 2020). However, tracking animal movement in zoos presents technical and ethical challenges. While GPS collars are widely used in field studies, their use can be invasive, requiring anaesthesia or extensive training (Horback et al. 2012; Brink et al. 2013). Moreover, GPS data may be imprecise, especially during stationary behaviour (Gunner et al. 2022), and wearing a collar can itself influence animal behaviour. In addition to GPS, apps can be used to record the position of the animal within the enclosure on a map. However, common solutions such as Zoo-Monitor use maps that are not true to scale (Wark et al. 2019). This makes it difficult to determine the distance travelled by an animal or the size of its home range. To address these limitations we developed a mobile application called Zoo-Observer (which can be obtained from the corresponding author), which allows observers to record both spatial and behavioural data directly and non-invasively. Using a tablet interface, observers can annotate the animal's positions and concurrent behaviours on a digital true to scale map of the enclosure. This approach enables precise, non-invasive analysis of spatial behaviour, including movement distances and home range use, offering a practical alternative to traditional tracking tools.

In this study, we used the Zoo-Observer app to monitor the enclosure use of three herbivore species, Rothschild's giraffe *Giraffa camelopardalis rothschildi*, Grant's zebra *Equus quagga boehmi*, and blue wildebeest *Connochaetes taurinus taurinus*, cohabiting a savannah exhibit at Opel-Zoo in Kronberg, Germany. This savannah enclosure includes areas of natural vegetation and several feeding sites, which were systematically relocated during the study in order to assess the influence of such changes on animal behaviour and space use. The observed species differ in terms of body size, digestive system and foraging behaviour, making them particularly relevant for investigating space use and interspecific interactions in a mixed-species setting. In addition to these behavioural and ecological traits, their distinct feeding ecologies are especially relevant when examining the effects of feeding site manipulation. Giraffes, as browsers, primarily exploit alfalfa hay in this exhibit as a surrogate for leafy forage, whereas zebras and wildebeests are grazers. Wildebeests and giraffes are ruminants while zebras are hindgut fermenters, physiological differences that influence feeding frequency, digestion strategies, and potentially the spatial distribution of feeding effort. These species-specific

dietary needs suggest that the impact of relocating feeding sites may not be uniform across species but may alter interspecific dynamics at shared resources depending on accessibility and proximity to preferred substrates. Understanding these species-specific responses is essential for designing enclosures that support both welfare and natural behaviour.

By linking behavioural observations with fine-scale positional data across multiple species and over time, this study demonstrates how spatial tracking can reveal patterns that are otherwise difficult to detect. These include species-specific preferences for certain zones within the enclosure, indicators of inter- or intraspecific avoidance, signs of spatial exclusion, changes in movement patterns due to life history events (e.g., rearing of offspring), and the impact of environmental modifications such as relocation of feeding sites. Such insights are essential for identifying potential welfare concerns and for developing targeted, evidence-based enclosure designs and enrichment strategies. Offspring were born in all three species living in the savannah exhibit in 2019, offering a unique opportunity to examine how group dynamics and enclosure use shift over time. Juvenile presence may influence movement patterns, social interactions, and access to resources, justifying a temporal comparison between two consecutive years.

This study therefore addresses the following research questions:

1. Does relocating feeding sites influence enclosure use or activity budgets?
2. How does enclosure use change over a period of two years, considering the presence of offspring in the second year?
3. Which species or individuals access specific food resources most frequently?

To explore these dynamics, we applied a comparative observational design over two years, including periods before and after the birth of offspring and across different configurations of food placement. This approach enables the assessment of both temporal and situational variation in enclosure use and behaviour. Combining traditional ethological observations with systematic spatial mapping using the Zoo-Observer app the study provides a comprehensive, non-invasive framework for evaluating space use and animal welfare in complex, mixed-species zoo environments.

Methods

Study site and focal animals

Data were acquired at Opel-Zoo Kronberg (Germany) in September 2018 and from May to July 2019. At that time, the savannah enclosure was inhabited by three Rothschild's giraffe (one male, two female), three Grant's zebra one male, two female) and three blue wildebeest (one male, two female). A group of impalas *Aepyceros melampus* was also present in the enclosure but was excluded from data collection, as they were often out of sight and no offspring were born during the observation period. The impalas have their own separate area (upper right corner in Figure 1) to which they can retreat and where they are no longer visible to the observer. In 2019, one juvenile was born in each of the observed species. However, these offspring were excluded from the analyses, as no comparable pre-birth data from 2018 were available. The primary rationale for comparing the two observation periods, despite potential seasonal variation, was to assess how group dynamics and enclosure use may shift following the birth of offspring. Although the periods represent different seasons (early autumn vs. late spring to summer), the average daytime temperatures were comparable (2018=14.7°C; 2019=16.3°C), and observations were restricted to dry days between 0830 and 1730 to minimize weather-related variability.

During the studies in 2018 and 2019, the location of the hay provided for zebras and wildebeests was intentionally varied. This change aimed to assess the effect of feeding site location on space

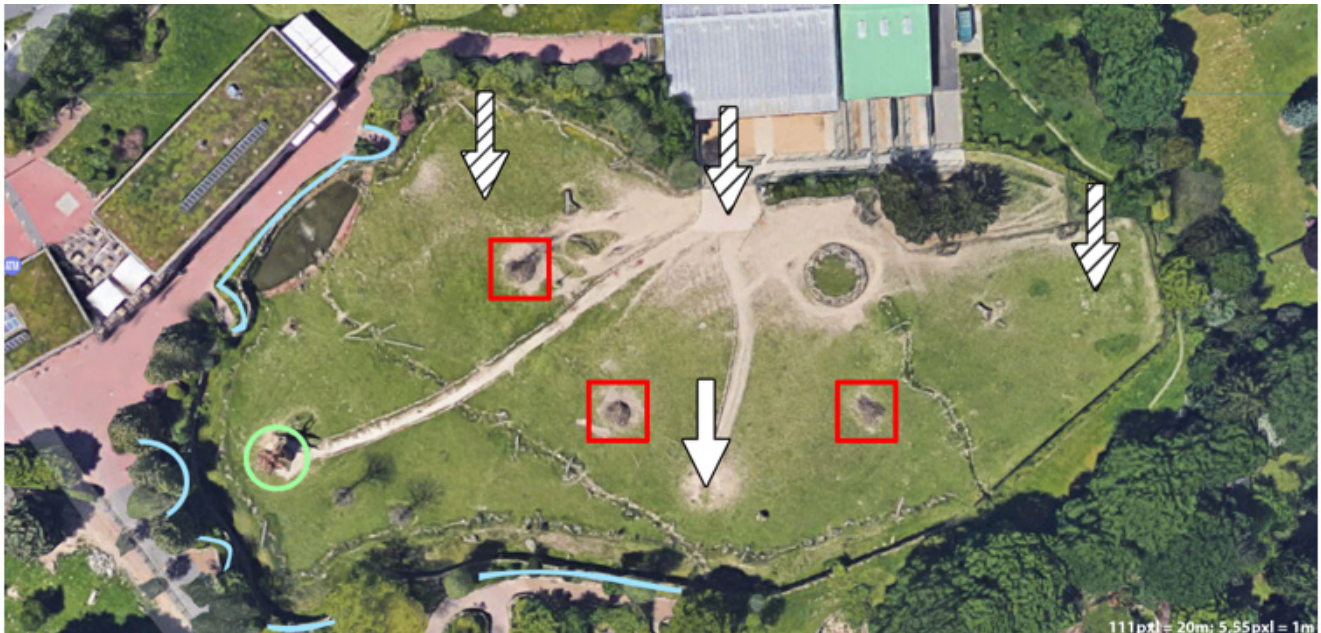


Figure 1. Satellite view of the savannah enclosure from Google Maps (Image® 2022 AeroWest, GeoBasis-DE/BKG, Maxar). The feeding grounds are marked as follows: red rectangles=branches and leaves; green circle=alfalfa hay; white arrows=hay. The hatched white arrows show the relocation of the haystacks. Areas, where visitors can see the savannah enclosure, are marked in light blue.

use and behavioural patterns. In contrast, alfalfa hay was provided in elevated hanging bags that were only accessible to giraffes and remained in a fixed location due to the species-specific feeding design. Fresh branches were provided in specific areas that were accessible to all species. As these branches were not completely eaten and remained at the feeding sites for longer, it was not been sensible to relocate this food source. Therefore, they were not treated as experimental variables. The allocation of hay feeding sites was carried out at certain intervals. Care was taken to ensure that at least two to no more than four days elapsed between laying the hay feeding sites, and placing the hay at the normal feeding site. Experimental days on which the hay was allocated always took place on two consecutive days. Three treatment conditions were defined as (1) hay in the standard position, (2) hay relocated to a new area, and (3) hay available simultaneously in the standard and a relocated position.

Locations were chosen to systematically vary the spatial distribution across the enclosure, including areas differing in exposure, proximity to shelter, and distance from the central giraffe feeding zone (Figure 1).

Data collection

Data were collected using scan sampling as the sampling rule and instantaneous sampling as the recording rule (Bateson and Martin 2007). Behavioural observations were conducted at one-minute intervals during continuous observation sessions. Data collection occurred twice daily in three-hour blocks between 0830 and 1730. Efforts were made to ensure balanced representation of the data across the morning (0830–1130), midday (1130–1430), and afternoon (1430–1730) periods. In 2018, observations were conducted on 12 days. In 2019, data collection varied by species due to observer availability and logistical constraints: giraffes were

observed on 23 days, zebras on 40 days, and wildebeests on 39 days. During each observation period, the observer recorded both the position of each animal on a digital map and the corresponding behaviour, using the Zoo-Observer app. The ethogram used in the app included the following key behavioural categories: stand, rest, move, eat and out of sight. These behaviours were selected based on their relevance to animal welfare and their suitability for comparison with activity budgets observed in the wild.

Zoo-Observer-App

The Zoo-Observer app was installed on Lenovo Yoga Tab3 tablets (Lenovo group Ltd, Hong Kong, China). A brief overview of how the app works and how it is structured can be found in the following section:

The Zoo-Observer app enables you to link observed behaviours directly to precise spatial positions on a digital map. The map can be calibrated to scale, enabling calculations of distances and movement paths. Since it is necessary to adapt the recording rules to the specific conditions, the sampling and recording rules are implemented in the application based on the definition of Bateson and Martin (Bateson and Martin 2007).

It is possible to choose from the following four options:

1. Focal Sampling: Focuses on one individual, with continuous recording of behaviour and location whenever changes occur. Data is confirmed by marking the position on the map.
2. Scan Sampling: Observing multiple individuals at set intervals. A timer, customizable in the settings, displays the current interval. Behaviours and locations are recorded during each interval and saved when the timer ends.
3. Multi-focus: Allows continuous observation of several individuals, ideal for small groups with infrequent behaviour changes. Data is recorded similarly to focal sampling.

4. Multi-focus Split: Functionally identical to multi-focus but uses a scan-style user interface.

The user interface during data acquisition depends on the selected acquisition mode, as shown in Figure 2. However, the

recording process is similar for all modes.

Data analysis

To calculate the distance covered by each animal, the Zoo-Observer app automatically computes the linear distance between successive positional data points using the euclidean distance.



Figure 2. Selecting a recording mode determines the user interface used for data recording and specific default settings. With focal sampling and multi focus, the individuals (dark blue) and behaviours (purple) are displayed next to each other in columns. The map can be accessed by tapping on the "next" button (green). In scan sampling and multi focus split mode, the individuals are arranged in rows. The ethogram is displayed under every individual. This has the advantage that the corresponding behaviour can be quickly selected for every individual. Non-displayed behaviour can be achieved by scrolling to the left. Each row of an individual has its button to access the map and indicate the position of the animal (green). Timer (light blue) and interval counter (red) are activated by default only in scan sampling mode but can be activated in all modes via the settings.

These distances are then summed for each observation session, providing an estimate of total distance travelled per animal. This value reflects the accumulated straight-line movement between all recorded locations during the sampling period. All statistical analyses were performed using MathWorks MATLAB 2020a (The MathWorks Inc., Natick, MA, USA). Positional data were used to compute heat maps of enclosure use. The enclosure map was divided into 50×25 quadrants, and the number of data points per quadrant was determined in order to identify the areas of the highest density of use. For each animal on each observation day, the centre of mass of the spatial data points was calculated by identifying the most densely used quadrant, doubling its area, and then calculating the weighted average of all the data points within the expanded area, to better reflect the spatial clustering around the main activity centre. This minimised distortion from adjacent high-use zones, ensuring that the calculated centre of mass reflected true location preference rather than being overly narrowed or diluted by less relevant points. To assess enclosure use, we calculated the 90% isopleth around the centre of mass, analogous to home-range estimation in wildlife studies (Börger et al. 2006). This served as a proxy for how broadly or narrowly an individual utilized the enclosure space on a given day.

To assess behavioural differences between the three experimental conditions (standard, relocated, both) we conducted a permutation-based analysis of variance (ANOVA) for each individual. The null hypothesis tested was that the mean values of the respective variables (distance travelled in km/h or the proportion of 'move' behaviour) did not differ between conditions.

Permutation-based ANOVA was chosen because, unlike

classical parametric ANOVA, it does not rely on assumptions of normality or the independence of repeated observations. This makes it more appropriate for our study design, which involves repeated measures within individuals. Given the small sample size and the potential deviations from normality, we applied an exact permutation procedure (perm="Exact") to the ANOVA. This approach does not rely on parametric assumptions and provides accurate p-values for hypothesis testing in such circumstances.

Analyses were carried out in R (version 4.5.1; R Core Team) using the lmpPerm package. Changes in enclosure use were assessed by comparing shifts in the centre of mass of the animal under different feeding site conditions. As each individual is represented by only one value per condition, no statistical comparisons were conducted for home range or centre of mass. Instead, spatial changes were evaluated descriptively and interpreted based on the visual inspection of heat maps and the calculated shifts in centre of mass.

Results

Relocating hay

Relocating the haystacks did not lead to notable changes in enclosure use in giraffes (Figure 3) and wildebeests (Figure 4). Both their home ranges and frequently used areas, as illustrated by the heat maps and calculated centres of mass, remained largely stable across conditions. Giraffes most frequently used the area containing alfalfa hay and one feeding area containing branches and leaves, regardless of the treatment conditions, with the exception of cow 2 which was most frequently near the barn

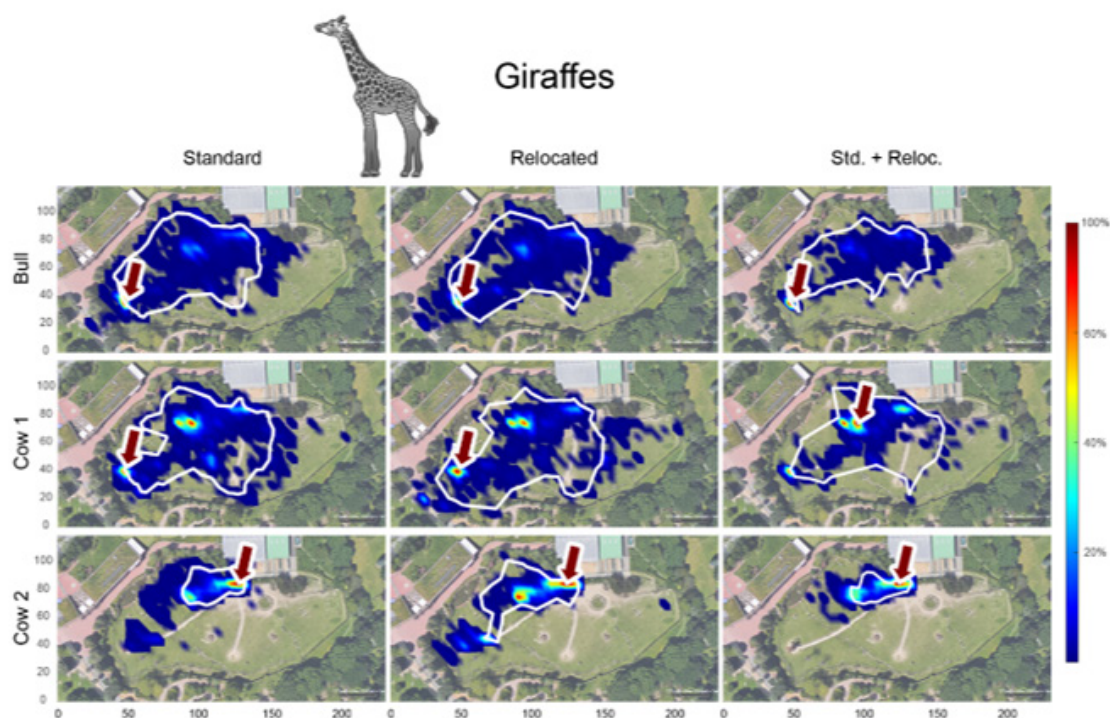


Figure 3. Enclosure use of the giraffes with standard set-up (left; $n=17$ days per individual), relocated haystack (middle; $n=12$ days per individual) and hay at the standard position and additionally at a relocated position (right; $n=6$ days per individual). The white line covering 90% of the data points represents the home range of the animals. X- and Y-axis indicate the size of the enclosure in metres. The colour coding of the heat map is given in position data per quadrant. The highest number of position data in a quadrant corresponds to 100%. The calculated centre of mass is indicated by the red arrow. Standard=standard hay position; Relocated=relocated hay; Std.+ Reloc.=hay in standard and relocated positions.

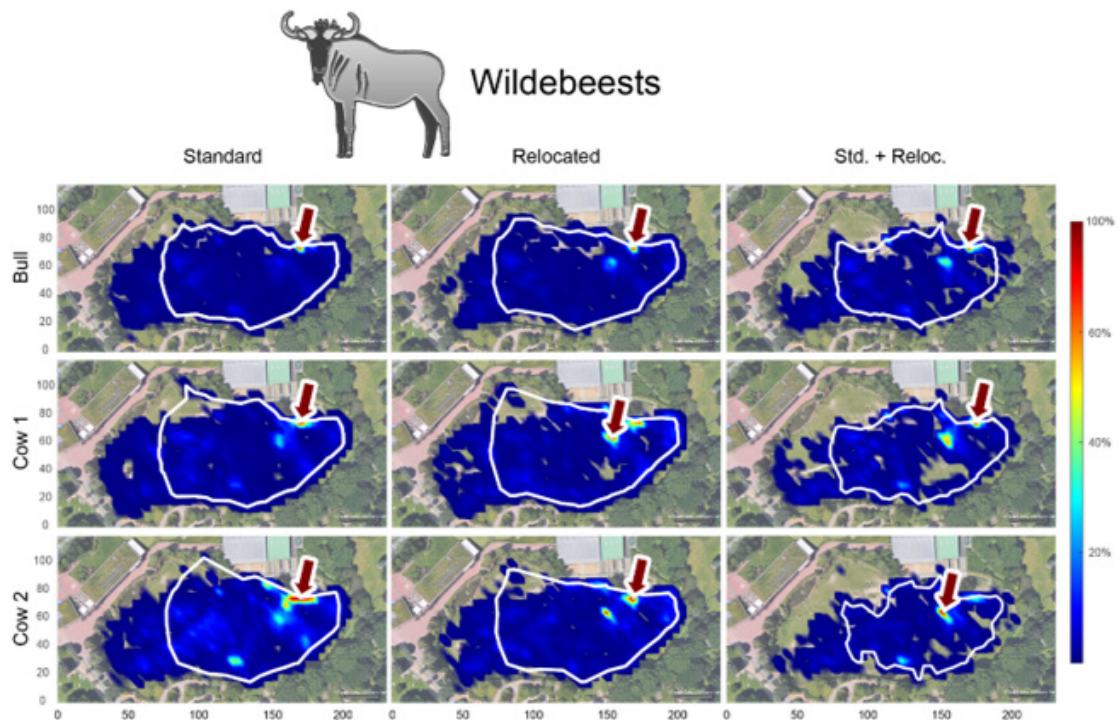


Figure 4. Enclosure use of the wildebeests with standard set-up (left; n=26 days per individual), relocated haystack (middle; n=16 days per individual) and hay at the standard position and additionally at a relocated position (right; n=9 days per individual). The white line covering 90% of the data points represents the home range of the animals. X- and Y-axis indicate the size of the enclosure in metres. The colour coding of the heat map is given in position data per quadrant. The highest number of position data in a quadrant corresponds to 100%. The calculated centre of mass is indicated by the red arrow. Standard=standard hay position; Relocated=relocated hay; Std.+Reloc.=hay in standard and relocated positions.

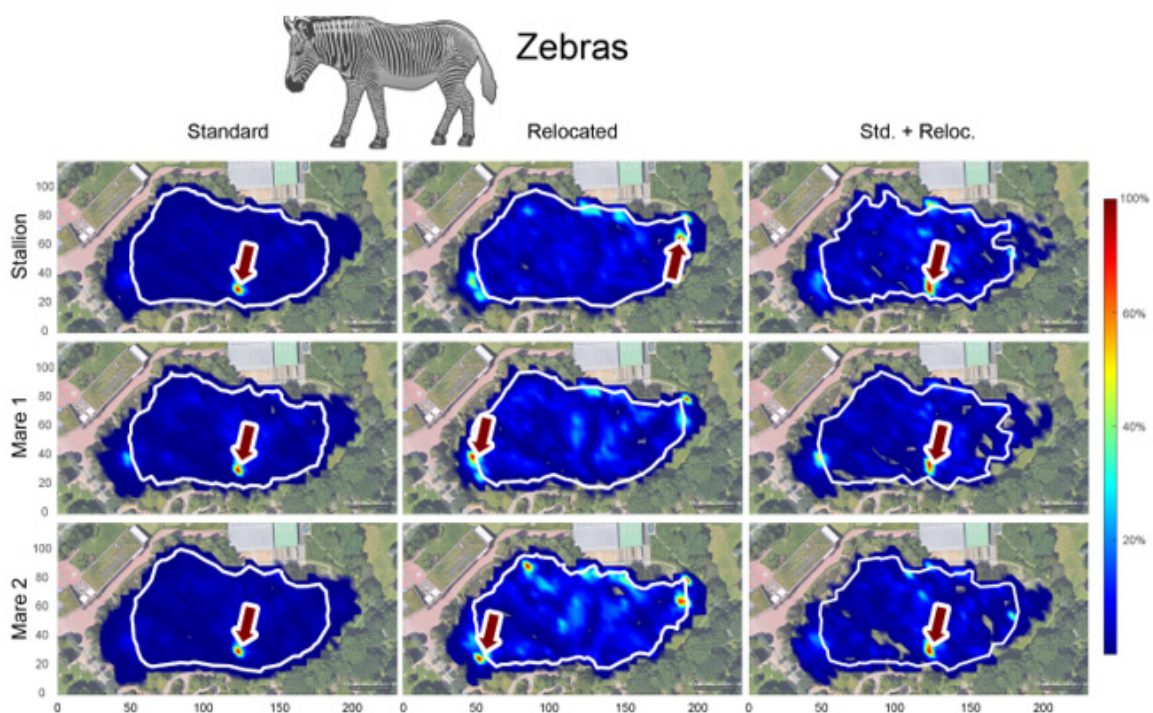


Figure 5. Enclosure use of the zebras with standard set-up (left; n=25 days per individual), relocated haystack (middle; n=18 days per individual) and hay at the standard position and additionally at a relocated position (right; n=9 days per individual). The white line covering 90% of the data points represents the home range of the animals. X- and Y-axis indicate the size of the enclosure in metres. The colour coding of the heat map is given in position data per quadrant. The highest number of position data in a quadrant corresponds to 100%. The calculated centre of mass is indicated by the red arrow. Standard=standard hay position; Relocated=relocated hay; Std.+Reloc.=hay in standard and relocated positions.

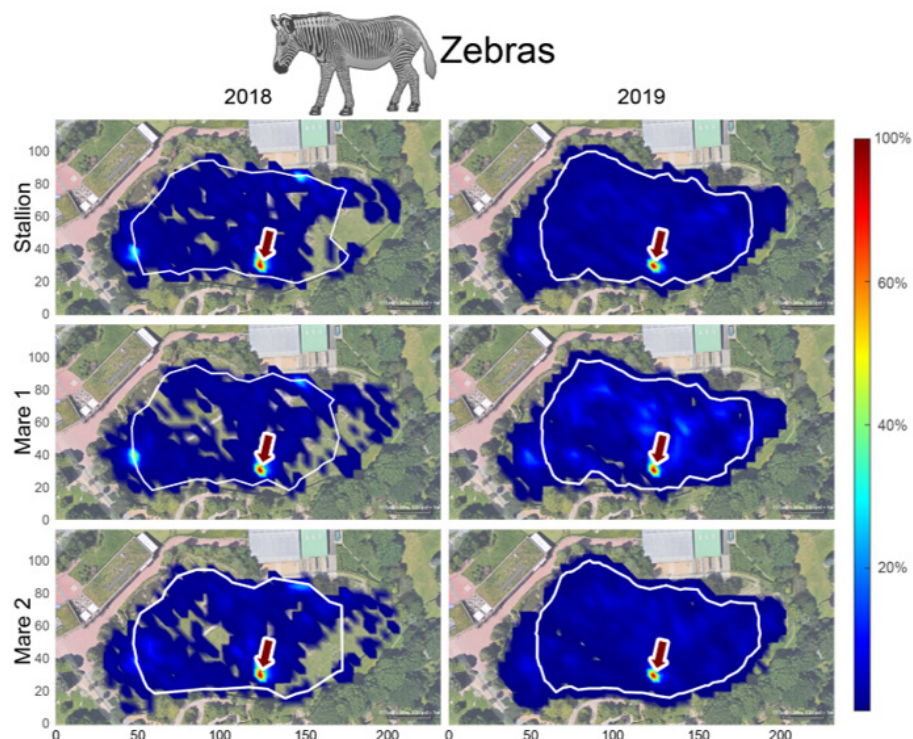


Figure 6. Enclosure use of zebras in 2018 ($n=5$ days per individual) and 2019 ($n=20$ days per individual). Only data points where no feeding ground relocation took place are shown. The white line covering 90% of the data points represents the home range of the animals. X- and Y-axis indicate the size of the enclosure in metres. The colour coding of the heat map is given in position data per quadrant. The highest number of position data in a quadrant corresponds to 100%. The calculated centre of mass is indicated by the red arrow.

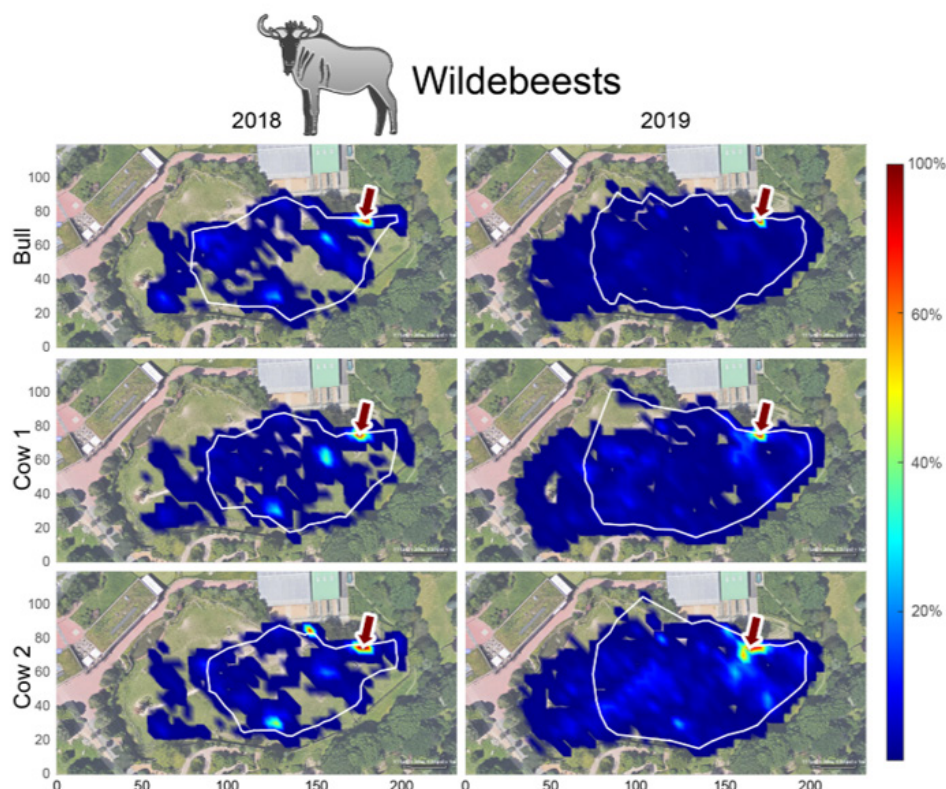


Figure 7. Enclosure use of wildebeests in 2018 ($n=5$ days per individual) and 2019 ($n=21$ days per individual). Only data points where no feeding ground relocation took place are shown. The white line covering 90% of the data points represents the home range of the animals. X- and Y-axis indicate the size of the enclosure in metres. The colour coding of the heat map is given in position data per quadrant. The highest number of position data in a quadrant corresponds to 100%. The calculated centre of mass is indicated by the red arrow.

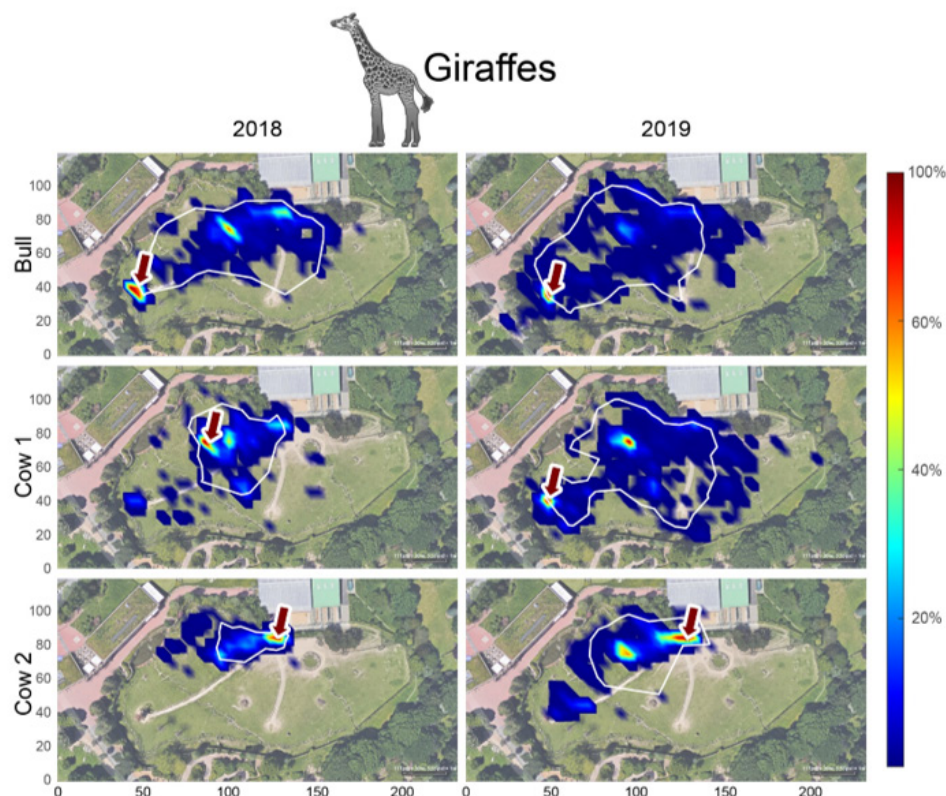


Figure 8. Enclosure use of giraffes in 2018 ($n=5$ days per individual) and 2019 ($n=12$ days per individual). Only data points where no feeding ground relocation took place are shown. The white line covering 90% of the data points represents the home range of the animals. X- and Y-axis indicate the size of the enclosure in metres. The colour coding of the heat map is given in position data per quadrant. The highest number of position data in a quadrant corresponds to 100%. The calculated centre of mass is indicated by the red arrow.

entrance. For zebras, although home range sizes were comparable across feeding setups (Figure 5), the spatial distribution of their most frequent locations shifted towards the new haystack positions, as shown in the heat map.

Long-term changes

Only data with no feeding ground relocation were used for long-term changes. No major long-term changes in enclosure use were observed between 2018 and 2019. Home ranges and most frequently used areas of all three species remained consistent each year (Figures 6–8). A notable exception was giraffe cow 1, whose home range in 2019 extended further into the area containing the alfalfa hay, compared to 2018 (Figure 8).

Activity budget and covered distance

To assess potential effects of haystack relocation on movement activity, permutation-based ANOVAs were conducted separately for each individual (Figure 9, Table S1). No significant differences were found between treatments (Table S1), indicating that the location of feeding site had no measurable effect on the animals' activity budgets. Similarly, no significant differences were detected in the distance covered per hour across conditions for any of the animals (Figure 10, Table S2).

Discussion

The analysis highlights the benefits of the app used in the study, which effectively records detailed behavioural data, animal positions and travelled distances. By providing accurate and comprehensive insights into animal responses to environmental changes without significantly interfering with them, as methods like GPS data collection do, the app enables accurate tracking and analysis of animal behaviour and movement patterns. This is essential for making informed decisions about management and welfare in captive environments. However, displaying position data alone does not reveal where the animals spend most of their time. Using heat maps and calculating the centre of mass makes it possible to identify the areas of the enclosure that are used most frequently. Additionally, tracking the distance travelled by the animals provides valuable insight into their activity levels.

Effects of hay relocation

Relocation of hay feeding sites had no discernible effect on the enclosure use of the animals and did not result in any significant changes in their movement activity (see behaviour "move" in Table S1), or distance travelled for giraffes, wildebeests, or zebras. Giraffes continued to feed at their stationary alfalfa hay feeder as well at the feeding area containing branches and leaves and

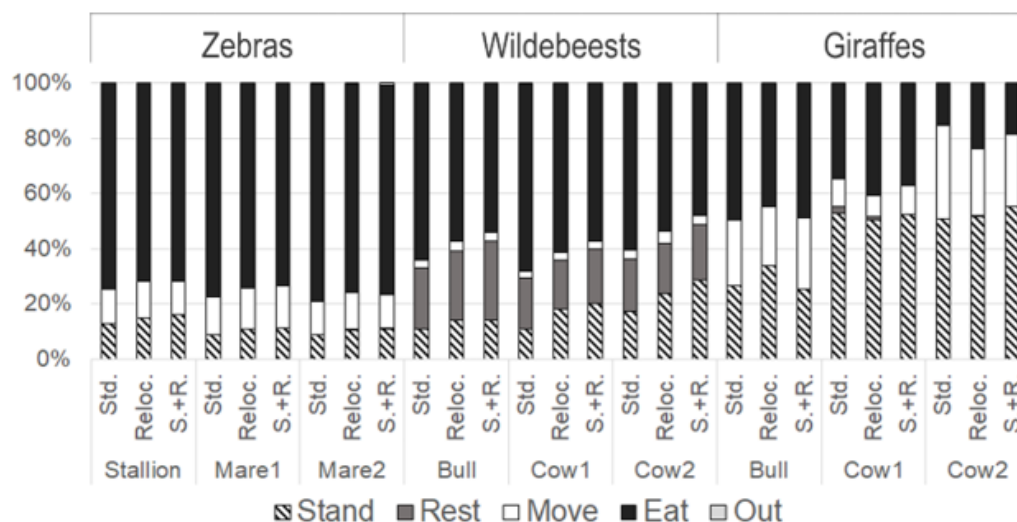


Figure 9. Mean percentages of behavioural categories across treatment conditions. Abbreviations: Std.=standard hay position; Reloc.=relocated hay; S+R=hay in standard and relocated positions. Number of observation days per condition and species: Zebras (Std.=25, Reloc.=18, S+R=9); Wildebeests (Std.=26, Reloc.=16, S+R=9); Giraffes (Std.=17, Reloc.=12, S+R=6).

therefore showed no meaningful response to the relocation of the hay racks used by the grazing species. Among the grazers, only zebras exhibited notable changes in spatial behaviour, particularly a shift in their most frequently used areas towards the relocated hay sites.

In contrast, wildebeests showed little response, which may be due to their preferred use of a resting area located far from visitor zones (Figures 1 and 7). The behavioural data confirm that this location is primarily used for resting. Although both zebras and wildebeests are grazers (Groves et al. 2009; Rubenstein 2009), only zebras consistently used the new feeding sites. One possible explanation is competitive exclusion, as zebras may exert social dominance over wildebeests (observation and statement from the animal keepers) in this enclosure setting. Furthermore, their differing digestive physiologies may contribute to this response:

zebras, being hindgut fermenters, need to forage more frequently and do not ruminate, which may increase their motivation to remain near hay sources (Janis 1976; Owen-Smith and Goodall 2014). The spatial overlap of the species' home ranges remained stable. However, it cannot be ruled out that the increased use of the new hayrack areas by zebras influenced the movement behaviour of giraffes and wildebeest. The temporal utilisation of certain areas may have changed; for example, while the zebras used the new hayrack areas, the wildebeest may have used areas that were free at that time. However, the total area utilised by each species remained unchanged. The wildebeest's most frequently used area also remains the same. The results highlight that a simple management intervention (e.g., relocating feeding sites) can have species-specific behavioural effects. While zebra responded to the change by shifting their spatial focus toward

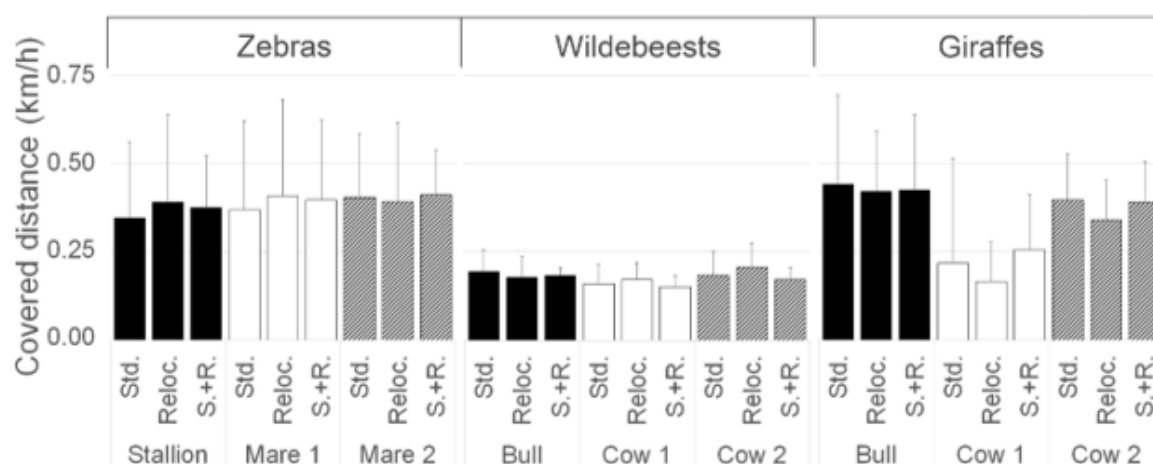


Figure 10. Mean distances covered (km/h) per treatment condition with standard deviations. No significant differences were found. Observation day counts are the same as listed in Figure 9.

the new feeding location, wildebeest showed little change in their use of space or activity levels, despite sharing a similar grazing ecology. These contrasting responses underscore that species with overlapping ecological niches do not necessarily react similarly to environmental manipulations. This has direct implications for zoo management, as feeding site changes might unintentionally reinforce social hierarchies or lead to unequal access. Moreover, the lack of measurable change in giraffe behaviour supports the conclusion that observed changes were specific to animals directly affected by the relocated resource. These findings illustrate the potential and the limitations of spatial modifications as a tool to influence animal movement and enclosure use, stressing the need for evidence-based, species-tailored husbandry decisions.

Due to the study design, which involved only one centre of mass and home range value per individual per condition, statistical comparisons were not feasible. Performing inferential statistics on such singular, non-replicated data points would violate the fundamental principles of statistical testing and could lead to misleading conclusions. Instead, we relied on descriptive analyses and visual inspection, which are both appropriate and commonly applied in comparable studies with low sample sizes or strongly individual-based data structures (Kuhar 2006; Hashmi and Sullivan 2020). In conclusion, we demonstrate that relocating feeding sites can have species-specific effects. Zebras showed notable spatial shifts, whereas wildebeests and giraffes exhibited minimal behavioural changes. These differences are likely due to social dynamics, digestive physiology, and resource-use preferences, and highlight the importance of tailoring management to specific species in zoo environments. Despite limitations in the statistical analysis, the findings emphasise that even simple interventions can have an uneven impact on species with overlapping niches, underlining the importance of evidence-based husbandry decisions.

Annual comparison (2018 vs. 2019)

Although no evident year-on-year changes were observed in enclosure use for any species, minor individual differences in home range shape and size were noted, particularly among the giraffes (Figure 8). For instance, the bull and cow 2 exhibited slight expansions in their home ranges between 2018 and 2019. However, these changes were subtle, and their respective centres of mass remained stable, indicating no fundamental change in their core area of use. The only individual whose centre of mass shifted was Cow 1, who expanded her use to the alfalfa hay area in 2019. Notably, she was not the female that gave birth that year. Even if this giraffe was not the calf's mother, there may still be a connection between them. While most behavioural studies focus on maternal responses, there is growing evidence that non-maternal giraffes also engage socially with calves present. For instance, Zoelzer et al. (2020) observed allonursing among non-mothers in captive giraffe herds, indicating cooperative care and nursery-group. Muller and Harris (2022) also highlight that adult females sometimes support calves that are not their own. Nevertheless, all interannual differences should be interpreted with caution, given that the data volume was substantially greater in 2019. Longer observation periods can result in more comprehensive coverage of an animal's activity range, which can exaggerate apparent changes in spatial use.

Overall, the results suggest a relative consistent pattern in spatial behaviour across years, with some individual variation that may reflect minor behavioural flexibility or sampling-related effects. It should also be noted that juvenile births did not appear to meaningfully alter overall enclosure use patterns. However, these results should be interpreted with caution due to limitations such as the season in which the data was collected and the focus on key behaviours, which resulted in the exclusion of behaviours

such as social interaction. Ideally, future studies should aim to include social interactions and their spatial positioning over years and seasons to better understand how changes in the enclosure propagate through group dynamics.

Activity and movement patterns

Combining movement duration and travelled distance yielded deeper insights into species-specific activity patterns. Although wildebeests occupied larger home ranges (Figure 7), giraffes actually travelled greater distances (Figure 10). This confirms that home range size alone does not reflect activity level. Giraffes, for example, showed relatively high movement activity (mean "move"=20.38%; Figure 9, Table S1), exceeding field-based estimates of 12% daily movement (Veasey et al. 1996). In contrast, wildebeests displayed limited movement during observation periods, consistent with their crepuscular activity in the wild (Berry, 1997; Maloney et al. 2005; Selebatso et al. 2017). Their higher proportion of grazing (58.18%) and lower proportion of resting (20.93%) compared to their wild counterparts (Ben-Shahar and Fairall 1987; Berry 1997) likely reflects both species differences and the observation period (0830 to 1730). Zebras exhibited mean movement rates of 0.47 km/h, closely matching wild foraging rates of ~0.5 km/h (Owen-Smith and Goodall 2014). This suggests that the enclosure may already promote species-typical movement patterns, and raises the question of whether increasing activity through enrichment would be beneficial or even necessary. The goal of husbandry interventions should therefore not be increased activity per se, but rather the promotion of species-appropriate patterns.

Animal welfare

Animal welfare assessments benefit from using multiple parameters. Covered distance is a particularly informative indicator, reflecting both physical exertion and behavioural engagement (McPhee and Carlstead 2012; Holdgate et al. 2016; Whitham and Miller 2016; Nyamuryekung'e et al. 2023). Higher activity levels, especially when they mirror wild-type movement patterns, can indicate good welfare and environmental suitability. Conversely, repetitive or abnormally limited movement may signal welfare concerns (Broom 1988; Jones et al. 2014). In this context, travelled distance offers clearer insights than home range alone, since the latter provides only spatial extent without frequency or intensity of use. Commercial apps like ZooMonitor or Prim8 often only track position, omitting valuable data on movement intensity and distance travelled (McDonald and Johnson, 2014; Wark et al. 2019). The Zoo-Observer app used here provides a more comprehensive dataset by combining spatial and behavioural information.

Refining animal welfare assessments through multidimensional spatial analysis

Zoo-Observer enables the extraction of multiple layers of information from positional data. This study demonstrates how positional data, when processed with complementary spatial tools, can yield insights beyond simple occupancy. Isopleths capture range, heatmaps highlight intensity, and walking distances quantify engagement. When combined with behavioural states, these metrics offer a multifaceted view of how animals use and experience space, offering a refined approach to future welfare assessments.

Methodological considerations and limitations

Several limitations must be acknowledged. First, data were collected across different seasons and in unequal volumes across years, which may confound temporal comparisons. As the impala herd living in the enclosure was not observed during the study,

no conclusions can be drawn about how they might respond to the relocation of the hay feeding site and the zebras' changed use of the enclosure. Although descriptive metrics were used appropriately given the data structure, future studies would benefit from quantitative approaches to assess spatial shifts, possibly through bootstrapped overlap indices or Bayesian modelling to accommodate individual-level data without replication. Focusing on key behaviours resulted in the exclusion of behaviours such as social interaction. Ideally, future studies should aim to include more behaviours and their spatial positioning in order to better understand how changes in the enclosure propagate through group dynamics.

Conclusion

This study highlights the impact of small-scale environmental modifications, such as the relocation of feeding sites on the behaviour of animals and their use of enclosures in a zoo setting. While the change influenced the spatial preferences of the zebras, other species showed minimal behavioural adjustments. This illustrates the importance of ecological traits in shaping responses to enclosure design. The findings suggest that feeding site management could be an effective, low-effort tool for encouraging enclosure use, provided species-specific needs and dynamics are considered. The study also found consistent enclosure use patterns over two years, indicating temporal stability. Although all observed species had juveniles in 2019, only a giraffe cow showed increased enclosure use, which could be linked to the presence of the juvenile, even though this giraffe was not its mother. This highlights the importance of considering life-history context when interpreting spatial data.

Crucially, the study emphasises the importance of collecting and analysing detailed positional data as an essential component of modern zoo research and welfare assessment. Beyond simple space-use metrics such as home range or heat maps, integrating movement-derived measures, especially total distance travelled, provides a more nuanced, quantitative insight into animal activity, energy expenditure and well-being. Our results show that how actively animals move within an enclosure cannot be captured with enclosure use alone. Giraffes, for instance, had smaller home ranges than wildebeests, yet travelled greater distances, indicating a higher level of physical engagement with their environment. Such distinctions are vital for accurately interpreting animal behaviour and assessing welfare. The Zoo-Observer app proved to be a practical, non-invasive tool for collecting fine-scale data allowing multifaceted analyses of behavioural patterns, movement intensity and spatial preferences. Integrating such tools into routine monitoring can enhance the evidence base for enclosure design and welfare strategies, supporting the delivery of individualised care and improving husbandry practices in modern zoological institutions.

Publication ethics

The study adhered to the EAZA Code of Ethics and advice on the husbandry of zoo and wildlife species in captivity. Consent was obtained from the owners for the participation of their animals in this study.

Conflict of interest

This research was conducted without any commercial or financial relationship that could be perceived as a potential conflict of interest.

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