Behavioral Time Budgets and Spatial Use of Captive Forest Reindeer *(Rangifer tarandus fennicus)*, Przewalski's Horses *(Equus ferus przewalskii)*, and Domestic Cattle *(Bos taurus)*

Beteendemönster och rumslig användning hos skogsvildren (*Rangifer tarandus fennicus*), Przewalskis häst (*Equus ferus przewalskii*) och nötkreatur (*Bos taurus*) i fångenskap

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Abstract

Understanding how animals in captivity allocate their time to different behaviors and utilize various areas within their enclosures is essential for improving animal welfare and optimizing enclosure design. This study examined time budgets for different behaviors, and use of space within enclosures in three species at Nordens Ark: forest reindeer (*Rangifer tarandus fennicus*), Przewalski's horses (*Equus ferus przewalskii*), and cattle (*Bos taurus*). Observations were conducted over a five-year period, and the data was analyzed to identify both species-specific and cross-species differences in behavior and spatial use. The statistical results revealed differences among species in both location use and behavior. The domesticated cattle spent significantly more time in artificial areas compared to the other breeds, reinforcing the idea that domesticated species, like cattle, may be better adapted to human-managed environments. The observational analysis highlighted some similarities among species, as sheltered areas and locations where resources such as food were placed were generally more frequently used. These patterns may be linked to resource placement and the design of the enclosures, which influence space utilization. The most prominent behavior observed was that all species spent a significant proportion of their time engaged in food-related activities. These findings highlight the importance of designing enclosures that address both species-specific and general needs for all three species. The results can not only contribute to improving animal welfare in captivity but also support conservation efforts by promoting behaviors critical for the reintroduction of threatened species, such as forest reindeer and Przewalski's horses, into the wild. Future studies could explore the impact of relocating food resources within enclosures to assess its effect on space utilization, informing optimal enclosure design and resource distribution.

Sammanfattning

Att förstå hur djur i fångenskap fördelar sin tid mellan olika beteenden och använder olika områden inom sina hägn är centralt för att förbättra djurvälfärden och optimera utformningen av hägn. Denna studie undersökte tidsbudgetar för olika beteenden samt platsanvändning hos tre arter vid Nordens Ark: skogsvildren (*Rangifer tarandus fennicus*), Przewalskis häst (*Equus ferus przewalskii*) och tamboskap (*Bos taurus*). Observationer genomfördes under en femårsperiod, och data analyserades för att identifiera både artspecifika och artöverskridande skillnader i beteenden och platsanvändning. De statistiska resultaten visade skillnader mellan arterna både i platsanvändning och beteende. De domesticerade nötkreaturen spenderade avsevärt mer tid i artificiella områden jämfört med de andra arterna, vilket förstärker idén om att domesticerade arter, som nötkreatur, kan vara bättre anpassade till människoskapade miljöer. Den observationsbaserade undersökningen visade också likheter mellan arterna, då skyddade områden och platser med resurser, såsom mat, användes frekvent. Dessa mönster kan kopplas till resursplacering och utformningen av inhägnaderna, vilka påverkar hur utrymmet utnyttjas. Det mest framträdande observerade beteendet var att samtliga arter tillbringade en betydande del av sin tid med födorelaterade aktiviteter. Dessa resultat understryker vikten av att utforma hägn som tillgodoser både artspecifika och generella behov för alla tre arterna. Fynden bidrar inte bara till att förbättra djurvälfärden i fångenskap, utan de stödjer även bevarandeinsatser genom att främja beteenden som är kritiska för återintroduktion av hotade arter, såsom skogsvildren och Przewalskis häst, i det vilda. Framtida studier kan undersöka hur flyttning av foderresurser inom inhägnader påverkar utnyttjandet av utrymme, vilket kan hjälpa till att optimera design och fördelning av resurser.

Introduction

Zoos play a crucial role in wildlife conservation, particularly through *ex situ* activities such as educational programs, captive breeding, and wildlife management. Recently, zoos have increasingly participated in *in situ* conservation efforts, collaborating with government agencies and local communities to support endangered species recovery (Tribe & Booth, 2003). When the goal is reintroduction into the wild, ensuring animals display natural behaviors is particularly important. (Hosey et al., 2009). Captive-reared animals, for instance, often experience higher predation rates compared to their wild counterparts, highlighting the importance of maintaining behaviors critical for survival (Prince, 1999). Sometimes, however, behavioral observations in the wild are not feasible. In such cases, behavioral studies conducted in zoos are essential for understanding the needs of animals, as such studies allow us to better understand species-typical behaviors and how animals interact with their environment. In addition, such studies can inform about factors that affect wellbeing in captivity (Hosey et al., 2009).

The spatial requirements of wild animals are influenced by the distribution and availability of resources such as food, water, shelter, and the frequency of social interactions (Prince, 1999). In captivity, where enclosures are typically much smaller than natural home ranges, it is important to design spaces that meet behavioral needs rather than simply replicating natural home ranges. Bothe size and complexity of enclosures play a critical role in animal welfare. While small enclosures can lead to increased aggression, pacing, and grooming, more complex, naturalistic environments encourage species-typical behaviors and reduce stress (Hosey et al., 2009). Enclosure utilization is also often uneven. Wild boar at the Rome Zoo, for example, spent most of their time in just two of the nine equally sized sections of their enclosure, favoring areas with mud, shade, and food provisioning while avoiding spaces near visitors. This suggests that species-specific biology, environmental preferences, and enclosure design significantly influence space use. It is therefore critical to incorporate habitat features that reflect species' ecological needs to ensure optimal welfare (Hosey et al., 2009).

Monitoring behavior is invaluable for assessing animal welfare in captivity. Animals have both physiological and behavioral needs, which include performing natural behaviors (Bracke & Hopster, 2006). If these needs are not met, animals may exhibit abnormal behaviors, such as stereotypies—repetitive, non-functional actions that are often caused by stress or inadequate environments (Hosey et al., 2009). Stereotypies remain an important welfare concern, although improvements in enrichment and enclosure design have made them less common in modern zoos (Hosey et al., 2009).

The study focuses on animal behavior, and as mentioned, food provisioning is a key factor influencing behavior. Food availability often dictates how animals allocate their time and energy, making it a critical component of understanding behavioral patterns. In the wild, animals spend a large proportion of their time foraging for food and water. In captivity, however, food is typically provided in a single location, reducing the time and energy spent on feeding behaviors. This can result in idle time and increase the likelihood of abnormal behaviors (Prince, 1999). Food-based enrichment strategies, such as scattering food or using feeding puzzles, are particularly effective in promoting natural foraging behaviors and reducing stress (Hosey et al., 2009; Prince, 1999). Moving animals between enclosures can sometimes cause stress, but it may also function as enrichment by encouraging exploratory behavior.

Naturalistic enclosures are often preferred, as they promote higher activity levels and reduced aggression compared to barren environments (Hosey et al., 2009).

In this study, both domesticated and wild animals living in a zoological park will be observed. Therefore, it is important to understand the differences between these groups, particularly regarding their adaptation to humans and the effects of domestication. This understanding can help determine how these factors influence their behavior in the zoo environment. The differences between wild and domesticated animals also influence their adaptability to captive environments. Domesticated animals have undergone genetic and environmental changes that increase their tolerance to handling and environmental variation, resulting in reduced emotional reactivity and improved reproductive success in captivity. However, despite these adaptations, domesticated animals retain many of their natural behavioral needs, which must be met to ensure welfare (Prince, 1999). Comparisons between domesticated animals and their wild counterparts can provide insights into critical welfare considerations and guide enclosure design (Hosey et al., 2009). In conclusion, behavioral studies in zoos provide essential insights into animal welfare and habitat use, informing improvements in enclosure design, environmental enrichment, and care practices. By understanding species-typical behaviors and individual preferences, zoos can create environments that better support the physical and behavioral needs of their animals. This is particularly important for species intended for reintroduction into the wild, as the ability to express natural behaviors is critical for survival (Wark et al., 2019). Differences between domesticated and wild animals further highlight the need for species-specific care and enrichment strategies to ensure high welfare standards in zoos (Hosey et al., 2009; Prince, 1999).

The aim of this study is to contribute to the understanding of how three different species allocate their time to various behaviors and utilize space within enclosures, with the goal of informing improvements in enclosure design that better accommodate the ecological and behavioral needs and animal welfare practices in a species-specific manner. Specifically, the study focuses on forest reindeer (*Rangifer tarandus fennicus*), Przewalski's horse (*Equus ferus przewalskii*), and three breeds of domestic cattle (*Bos taurus*) at Nordens Ark, a zoological park in southern Sweden. By quantitatively comparing the duration of specific behaviors and enclosure use among these species, this research seeks to identify species-specific patterns that can guide the development of care and enrichment strategies tailored to the needs of both wild and domesticated animals.

This study hypothesizes that there will be species-specific differences in both the time allocation to various behaviors and the utilization of enclosure space among forest reindeer, Przewalski's horse, and domestic cattle. Domesticated cattle, having undergone extensive adaptation to human-managed environments, are hypothesized to exhibit more distinct patterns of behavior and enclosure use compared to forest reindeer and Przewalski's horse. Furthermore, given that access to food is a primary behavioral driver, all species are expected to allocate a considerable amount of time to feeding-related behaviors. To investigate these hypotheses, statistical analyses were performed, complemented by observational graphs. Comparisons were made both between species, focusing on the time spent on specific behaviors and time spent in different areas of the enclosure, and within species, examining whether the species, as a whole, spent more time in certain areas of the enclosure than in other areas. Furthermore, by enhancing our understanding of species-typical behaviors and their expression in managed environments, this study may also inform in situ conservation efforts.

This includes supporting reintroduction programs and improving the survival prospects of animals released into the wild.

Method

Study area

The study took place at Nordens Ark, a zoological park operated by a non-profit foundation located in Hunnebostrand, Bohuslän, Sweden, Figure 1. The park, which is open to visitors year-round, was established in 1998 and is situated on the Åby Säteri estate. It encompasses a total area of 383 hectares, including pastures, forested areas, and animal enclosures (Nordens Ark, n.d.f), and houses around 60 species from various animal groups such as birds, mammals, reptiles, and amphibians (Nordens Ark, n.d.g). The aim of Nordens Ark is to protect endangered species and to stimulate sustainable use of biological resources. The organization focuses on conservation, breeding and husbandry, as well as research and education (Nordens Ark, n.d.f).

Nordens Ark prioritizes animal welfare by designing enclosures that enable species to exhibit natural behaviors. By studying each species' natural habitats and behaviors, they create spaces that replicate these conditions to meet their ecological and behavioral needs (Nordens Ark, n.d.i). Animal welfare is addressed through four key elements: providing appropriate nutrition, implementing behavioral enrichment, ensuring veterinary care with an on-site veterinarian, and designing enclosures that mimic natural habitats (Nordens Ark, n.d.h). Enrichment programs are tailored to the animals' natural behaviors and ecological needs, aiming to stimulate their physical and mental capacities. Tools such as food puzzles and scent-based activities are used to encourage foraging, exploration, and problem-solving, while enclosures are equipped to mimic their natural environments, allowing animals to maintain control over their surroundings and enhance their well-being (Nordens Ark, n.d.i).

The data I have collected is a part of a broader project initiated at Nordens Ark, where multiple observers have previously gathered behavioral data on Przewalski's horse, forest reindeer and domestic cattle. The project also includes data on the European bison (*Bison bonasus*), which has already been analyzed in a previous report. Building on this foundation, I have chosen to focus on specific research questions that align with Nordens Ark's overarching goals, such as investigating how behavior and habitat use differ between species. I conducted four observational studies myself, two on Przewalski's horses and two on forest reindeer, all of which were done in autumn 2024. The rest of the data was collected by other observers.

Figure 1. Map showing the location of Nordens Ark in Hunnebostrand, southwestern Sweden. Screenshot taken from Google Maps (https://www.google.com/maps), accessed on [January 2025].

Study species

Przewalski's horse is the last remaining truly wild horse species and has never been successfully domesticated. It became extinct in the wild during the 1960s due to hunting and competition with domestic livestock for access to water sources. For many years, Przewalski's horse existed solely in zoos until its reintroduction in the wild in 1992. Today, it can be found in three national parks in Mongolia, but the species remains critically endangered. Historically, Przewalski's horse roamed the vast steppes and saline deserts bordered by mountains in southwestern Mongolia. The species was present as far back as 8000 years ago, with evidence suggesting it once inhabited regions in France (Nordens Ark, n.d.a). One of Przewalski's horse unique adaptations is its ability to withstand water scarcity by storing fat in its neck, allowing it to survive extended dry periods, like camels. Physically, Przewalski's horse features a large head and a robust body, they weigh about 300 kg and have an upright mane and lack a forelock. Its coat is typically golden brown, complemented by black legs, mane, and tail. Within herds, a dominant mare typically leads the group, while the stallion defends the herd from potential threats and maintains his position against rival stallions (Nordens Ark, n.d.a).

According to Nordens Ark (n.d.b), the forest reindeer is currently found only in the wild in Karelia, Russia, and some adjacent areas in Finland. Historically, this species was not limited to Russia and Finland but was also present in Sweden. However, it became extinct in Sweden by the late 19th century, with the last recorded locations being Härjedalen and Torne Lapland. The decline in the forest reindeer's range is primarily attributed to hunting, as farmers are generally unwilling to allow these animals on their lands. It is still hunted in areas where the species remains, partly to prevent interbreeding with domestic reindeer. As the name suggests, the forest reindeer typically inhabits forested regions. Both males and females possess narrow, upright antlers that facilitate navigation through dense trees. Their diet consists mainly of buds and shoots in the spring, grasses and herbs during the summer and autumn, supplemented by mushrooms in the autumn. In winter, they primarily feed on lichens, which they scrape from beneath the snow using their hooves. Males weigh between 100-180 kg, while females weigh approximately 60-90 kg. The mating season occurs from September to October, with calves typically being born in May (Nordens Ark, n.d.b).

The three domesticated cattle breeds included in this study are the Rödkulla, Fjällnära cattle, and Väneko breeds. The Rödkulla is an ancient Swedish landrace breed, often characterized by its red coat and naturally hornless condition. Historically, this breed was found in regions such as Dalarna and the west coast in Sweden, as well as in Norway and Finland. The breed has been documented since at least 1842, and by the late 1930s, there were around 30,000 individuals in Sweden alone. Rödkulla cattle are dual-purpose, valued for both milk and meat production. A Rödkulla cow can produce over 5,000 liters of milk per year. However, modern dairy cows typically yield twice that amount, which may explain why the Rödkulla is currently considered critically endangered. Known for their lively temperament and good-natured disposition, Rödkulla cattle are free from hereditary diseases, have strong legs and hooves, and are known for easy calving and high fertility. Additionally, the breed is well adapted to cold climates, allowing it to remain outdoors for longer periods. They weigh between 350-600 kg (Nordens Ark, n.d.c).

The Fjällnära cattle is also a critically endangered breed, originating from the mountainous regions of northern Sweden (Norrland). Like the Rödkulla, this breed is known for its good health and friendly temperament. While it shares the same origins as a closely related breed, the Fjällko, Fjällnära cattle produce less milk. This is because they have not been selectively bred for higher milk yield and have not undergone targeted breeding programs. Due to their adaptation to mountainous regions, they can subsist on relatively sparse grazing. Since the 1990s, Fjällnära cattle have been recognized as a distinct breed. Like the Rödkulla, they are naturally hornless and are usually white with spots or patches in various colors and weigh between 250–450 kg (Nordens Ark, n.d.d).

The Väneko is a breed well-suited for natural pasturelands and can help preserve species-rich grasslands due to its ability to find and utilize diverse vegetation. The breed traces its origins to the South Swedish Allmoge cattle, which existed in southern Sweden during the Middle Ages. In 1992, a herd was discovered on a farm in Väne-Ryr, Västra Götaland, where the breed had been kept for over 100 years without crossbreeding with more specialized milk-or meat producing cattle. Väneko cattle have horns and come in a variety of colors, typically weighing around 500 kg (Nordens Ark, n.d.e).

Study design

The aim of this study was to investigate time allocation to different behaviors and location use among the three species mentioned above. By understanding how these species interact with their environment and distribute their behaviors, the study seeks to inform enclosure design and species-specific care practices. To achieve this, data were collected through observational studies conducted on the animals in their enclosures.

A smartphone equipped with an observation logging application was used to record behaviors. The observations were conducted over three to four hours, either in the morning (8:00–11:00/12:00) or in the afternoon (12:00–15:00/16:00). The observer arrived on-site at least five minutes before the start of data collection to locate the focal animal, though arriving earlier was advantageous to allow the animals to acclimatize to the observer's presence. All observations were made from outside the enclosure, and the observer never entered the animals' area or engaged in direct contact with them. The study was carried out between the years 2019 and 2024. A total of eight different observers participated in the study, but not all observed every species. Four observers were assigned to observe cattle, five observed reindeer, and all eight observed horses.

Before each observation session began, the observer, date, enclosure, and the focal animal were entered into the app. Only one focal animal was followed during each 3–4-hour behavioral analysis session. The individual to be observed was randomly selected, and the same focal animal was observed both in a morning session and in an afternoon session, though not on the same day. For each observation, a different focal animal was selected. However, as the study spanned five years and included multiple seasons, it is possible that the same animal was observed more than two sessions. Additionally, the composition of animals within the enclosures varied over time, and some observers may have had the opportunity to observe all the animals in the group before starting again. If the focal animal was lost from view, a new individual was randomly chosen from the group to continue the behavioral observation.

When the observation started, both the location and continuous behavior of the focal animal were logged. Location referred to predefined areas within the enclosure that had been previously categorized as "canopy", "tree area", "open", "roof", and "artificial", Table 1. Each time the focal animal moved to a new area, a new location was recorded in the app. Continuous behavior was also predefined with a set of common behaviors, though it could be supplemented with free-text entries for behaviors not represented in the app. Examples of behaviors include "standing only", "standing while ruminating", "walking only", "lying down with the head resting", "drinking". Any behavior lasting more than 10 seconds was logged under the "continuous" category in the app. Additionally, the observer could include comments in the app for later analysis, such as when a caretaker arrived or when the animals were being fed. If the focal animal moved out of sight or the observer was unable to clearly determine the behavior being performed at any point during the observation, both the continuous behavior and location were marked as "uncertain" in the app. At the end of the observation period, both the continuous behavior and location were logged as "end" to mark the observation's completion time. In total, 49 behavioral analyses were conducted on Przewalski's horses, 24 on forest reindeer, and 23 on domestic cattle. The observations were distributed across different seasons and years. The total observation time for time spent at different locations was approximately 205 hours for Przewalski's horses, 93 hours for forest reindeer, and 86 hours for cattle. For the behavioral analysis, the total observation time was 193 hours for Przewalski's horses, 92 hours for forest reindeer, and 88 hours for the different cattle breeds. The discrepancies between the observation times for location and behavioral analyses are due to the filtering out of "uncertain" observations.

Table 1. Overview of the total behaviors and locations included in the data analysis. The behavior "ruminate" was only recorded for forest reindeer and cattle breeds, as horses do not ruminate.

Behaviors	Locations
Defecate/ Urinate	Artificial
Drink	Canopy
Feed	Open
Lie down	Roof
Move	Tree area
Ruminate	
Scratch	
Self- grooming	
Smell	
Social interaction	
Stand	

Enclosures

The forest reindeer and Przewalski's horses were housed in separate enclosures at Nordens Ark and were occasionally moved to different enclosures during the study years. The group sizes varied slightly: the reindeer group consistently consisted of five individuals, while the Przewalski's horse group ranged from five to six individuals. The number of cattle in their group was less consistent, but it was estimated to typically include around ten individuals, with group sizes varying between five and fifteen. The sizes of the enclosures ranged from 2,400 to 7,400 square meters. The domestic cattle were kept in various natural grazing pastures (Figure 2) throughout the study period. Several of the enclosures were situated within the zoological park, with walkways passing by the enclosures where the animals were housed. These walkways typically passed by multiple locations within each enclosure, not just a single specific area, and were not expected to influence location usage. Some enclosures in the study were also located outside the park, where they were not accessible to visitors.

The enclosures were divided into distinct locations, as outlined in Table 1. Figure 3 illustrates an example of how different locations within an enclosure could appear. "open" was defined as areas with no trees or sparse tree cover. "Tree area" referred to areas with denser tree cover, within the reach of falling trees higher than 2m. "Artificial" represented man-made structures, often with gravel and feeding stations, while "roof" referred specifically to man-made structures with a roof providing shelter. "Canopy" was used when an animal was standing directly under the canopy of a tree, near its trunk. The enclosures varied in design and the sizes of these distinct locations varied across enclosures, with artificial and roofed areas generally being smaller compared to open and tree-covered areas. The animals were free to choose where they wanted to be within the enclosures, and since each observation session lasted 3–4 hours, individuals had sufficient time to move between different locations within their enclosure.

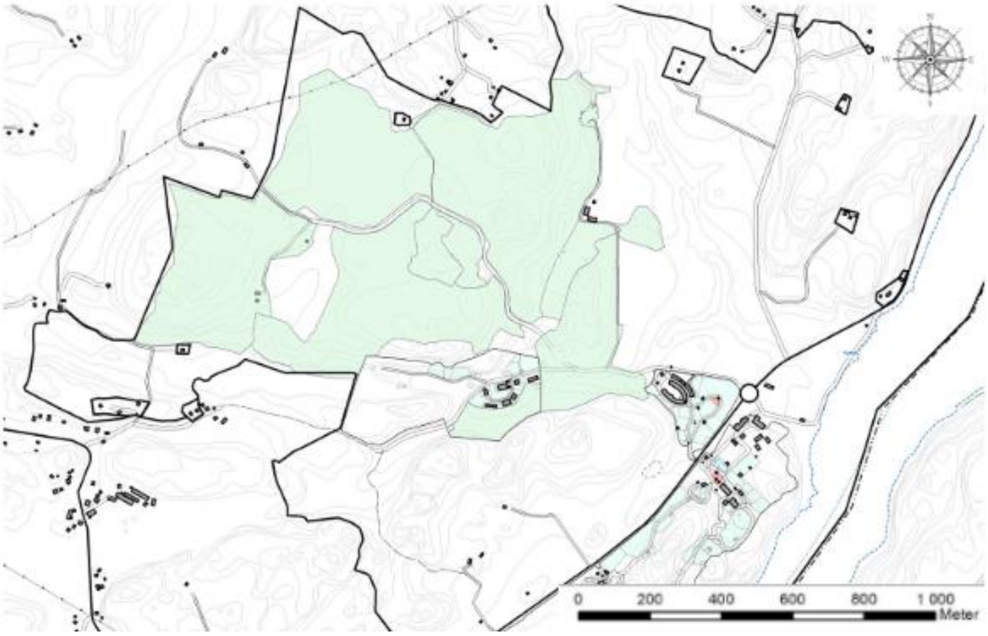

Figure 2. Overview of the natural grazing pastures marked in green and Åby Manor, outlined with a bold boundary. The different domestic cattle breeds utilized these enclosures across various natural grazing areas at Nordens Ark. Original image modified from Nordens Ark.

Figure 3. Picture 1 shows an example of an open area with trees in the background. Picture 2 depicts an artificial area with gravel and a feeding station in Przewalski's horses' enclosure. Pictures 3 and 4 are from the forest reindeer enclosure, showing a tree-covered area (3) and an open area (4). Photographed by the author, 2024.

Data Treatment

All observers followed the same template, entering data into standardized tables. In Excel, the duration of each behavior was calculated by measuring the time from the start of one behavior until the start of the next. The total duration of each behavior throughout the entire observation session was calculated by summing the durations of that behavior during the session. Similarly, the time the focal animal spent in each location was calculated by determining the time spent in one location before the animal moved to another location.

Next, certain related activities were merged into behavioral categories, to simplify data analysis. For example, "walk", "run", and "stroll" were combined into the category "move", while "standing while ruminating" and "lying down while ruminating" was combined into the category "ruminating", Table 1. The total times for each behavioral category and location in every observation were converted into percentages, summing to 100% per session. Additionally, the total time spent in each location and performing each behavior across all observations was summarized for each breed, ensuring a cumulative total of 100%. The data from every individual observation was used for statistical tests, while the summarized data (total percentages) was used to generate the graphs.

The category "uncertain" was excluded from these calculations, as it was not considered relevant to the analysis and only made up a small portion of the total time. To assess whether observations conducted on dates close to each other were more similar than those conducted further apart, autocorrelation was tested for each observation and species. Specifically, autocorrelation was assessed by calculating lagged correlations between consecutive observations, using time lags to measure the relationship between data points collected on different dates. This analysis helped determine whether the temporal proximity of observations influenced the observed data. No significant autocorrelation was detected (Appendix, Figure A1).

Comparisons were made to identify differences in location usage both between and within species, as well as differences in behavior between species. Multinomial logistic regression was used for the statistical tests because the dependent variables (such as behaviors or locations) were nominal and categorically distributed. This method is particularly suited for analyzing percentages distributed across multiple categories and can handle non-ordinal outcome variables, making it appropriate for the categorical nature of the data in this study. To facilitate these comparisons, the statistical models were run with different reference groups. For inter-species comparisons, all species ("forest reindeer", "Przewalski's horse", and "cattle breeds") were alternated as reference groups, one at a time. Reference groups provide a baseline category against which other categories were compared, enabling the detection of significant differences between groups. Additionally, all locations were alternated as reference groups to test for significant differences in location usage within species. Intra-specific differences in behavior were not tested statistically, as certain behaviors, such as standing, evidently occupy more time than others, such as drinking. Instead, the focus was placed on analyzing inter-specific differences in behaviors.

Significance levels were calculated for the relationships between variables, with p-values below 0.05 indicating statistically significant associations. The estimated coefficients revealed the strength and direction of these associations, with positive values indicating a positive relationship and negative values indicating a negative relationship. Model fit was evaluated using residual deviance and Akaike's Information Criterion (AIC). The statistical analyses were conducted using R version 4.2.3. ChatGPT was used to generate R code and assist in interpreting the output from R. Tables were created in Google Drive, and bar charts were produced in Excel.

Results

Inter-Species Statistical Comparison of Location Use

Przewalski's horses spent significantly less time in "artificial" than cattle did (β = -393.94, SE = 136.43, p <0.001). Cattle, on the other hand, spent significantly more time in "canopy" (β = 514.39, SE = 151.58, p < 0.001) and "roof" (β = 272.19, SE = 91.20, p = 0.003). In the comparison between Przewalski's horse and forest reindeer, horses spent significantly less time in "artificial" (β = -32.47, SE = 83.44, p < 0.001). However, they were found to spend significantly more time in "roof" (β = 155.17, SE = 81.71, p = 0.016). When forest reindeer were compared to cattle, reindeer spent considerably less time in "artificial" (β = -350.01, SE = 135.93, p = 0.009), Appendix Table A1-A3.

Within-Species Statistical Comparison of Location Use

When comparing habitat usage within the species for Przewalski's horse, the results indicated that when "artificial" were used as the reference category, horses showed significant preferences for "canopy" (β = -527.00, SE = 129.61, p <0.001) and "roof" (β = -200.92, SE = 75.82, p = 0.008) over "artificial". Przewalski's horse spent significantly more time in "artificial" (β = 424.18, SE = 109.02, p < 0.001) compared to "canopy". Similarly, when "canopy" was the reference category, horses showed a significant preference for "open" (β = 286.46, SE = 111.73, p = 0.010) and "tree area" (β = 398.91, SE = 109.20, p = 0.003) over "canopy". When "open" was used as the reference category, horses significantly preferred "artificial" (β = 170.28, SE = 71.42, p = 0.017) over "open", but showed significantly less preference for "open" (β = -331.00, SE = 124.43, p = 0.008) compared to "canopy". When "roof" was used as the reference category, horses exhibited a significant preference for "artificial" (β = 220.01, SE = 76.65, p = 0.004) and "tree area" (β = 179.93, SE = 62.97, p = 0.020) over "roof". Similarly, when "tree area" was the reference category, horses preferred "roof" (β = -170.06, SE = 77.61, p = 0.028) and "canopy" (β = -468.71, SE = 125.57, p < 0.001) over "tree area". Horses also significantly preferred "canopy" over "roof" (β = -339.10, SE = 138.24, p = 0.014), Appendix, Table A4.

When locations were compared within the cattle breeds, only one significant result was found. When "roof" was used as the reference category, cattle spent significantly more time in "roof" compared to "open" (β = 0.81, SE = 0.39, p = 0.039), Appendix, Table A5.

When comparing location use within forest reindeer, several significant differences were observed. When "artificial" was used as the reference category, reindeer spent significantly more time in "open" (β = 1.26, SE = 0.43, p = 0.003) and "tree area" (β = 1.32, SE = 0.43, p = 0.002) compared to "artificial". When "open" was used as the reference category, "artificial" (β = -1.14, SE = 0.43, p = 0.008) and "roof" (β = -1.12, SE = 0.43, p = 0.009) were used significantly more than "open". Additionally, when "roof" was the reference, "open" was used significantly less (β = 0.97, SE = 0.40, p = 0.017). When "roof" was the reference category, reindeer spent significantly more time in "roof" compared to "tree area" (β = 1.02, SE = 0.40, p = 0.011). When "tree area" was the reference category, forest reindeer spent significantly more time in "artificial" (β = -1.14, SE = 0.42, p = 0.007) and "roof" (β = -1.20, SE = 0.43, p = 0.005) compared to "tree area", Appendix, Table A6.

Inter-Species Statistical Behavioral Comparison

When comparing behaviors between cattle breeds and Przewalski's horses, cattle showed a significant positive tendency for feeding ($\beta = 0.27$, SE = 0.10, $p = 0.027$) but a significantly negative tendency for movement ($\beta = -0.40$, SE = 0.09, $p = 0.000$) and social interaction ($\beta = -0.88$, SE = 0.15, $p < 0.0001$). Additionally, standing was significantly less frequent in cattle compared to Przewalski's horses ($\beta = -0.3258$, SE = 0.1040, $p = 0.009$). When comparing Przewalski's horses to forest reindeer, horses exhibited significant positive selection for lying down ($\beta = 0.28$, SE = 0.10, $p = 0.026$), movement ($\beta = 0.30$, SE = 0.09, $p = 0.007$), social interaction ($\beta = 0.94$, SE = 0.08, $p < 0.0001$), and standing ($\beta = 0.29$, SE = 0.11, $p = 0.029$). Conversely, Przewalski's horses demonstrated significant negative tendency for feeding ($\beta = -0.61$, SE = 0.12, $p < 0.0001$), scratching ($\beta = -0.87$, SE = 0.24, $p = 0.002$), and self-grooming ($\beta = -0.79$, SE = 0.15, $p < 0.0001$). There were no significant differences in behavior between cattle breeds and forest reindeer, Appendix, Table A7-A9.

Observational Analysis of Location Utilization Across Species

The results indicate clear differences in habitat use among Przewalski's horses, forest reindeer, and cattle breeds, based on the percentage of time spent in each location. Przewalski's horses spent the largest proportion of time in "artificial" (30.37%) and "tree area" (25.00%). "Roof" was also used frequently (21.01%), followed by "open" (18.55%). The least utilized location for horses was "canopy", accounting for only 5.08% of their time. Forest reindeer primarily utilized "roof" (36.48%) and "artificial" (36.00%), showing a strong preference for these locations. Despite their name, they spent less time in "canopy" (19.45%) and minimal time in "open" (4.41%) and "tree area" (3.66%). Cattle displayed the strongest preference for "roof", which accounted for 42.94% of their total time. This was followed by "canopy" (20.62%), "tree area" (15.67%), and "artificial" (15.01%). The least used habitat for cattle was "open", representing only 5.76% of their time, Figure 4.

Observational Analysis of Behavioral Patterns Across Species

The results demonstrate distinct behavioral patterns among Przewalski's horses, forest reindeer, and cattle breeds based on the percentage of time spent on each behavior (Figure. 5). Przewalski's horses spent most of their time feeding (60.40%) and standing (22.85%), so these behaviors dominated their daily activity. Movement accounted for 9.96% of their time, while lying down represented 3.65%. Other behaviors such as social interaction (2.09%), smelling (0.32%), and scratching (0.16%) were less frequent. Similarly, minimal time was spent on drinking (0.54%), defecating/urinating (0.03%), and self-grooming (0.02%).

Forest reindeer exhibited a more balanced distribution of behaviors. Time spent feeding accounted for 25.82%, followed closely by standing (21.45%) and lying down (20.97%). Reindeer also devoted significant time to ruminating (18.72%) and moving (7.51%). Behaviors such as self-grooming (3.07%), smell (0.81%), and scratching (0.72%) were observed less frequently, with social interaction (0.04%) and defecating/urinating (0.15%) being rare.

Cattle spent the largest proportion of time feeding (35.32%) and ruminating (23.78%). Time spent standing was also considerable (24.12%). In contrast, lying down and moving accounted for 7.84% and 4.33%, respectively. Behaviors such as drinking (1.27%), smell (1.05%), and social interaction (0.93%) were observed infrequently. Minimal time was devoted to scratching (0.28%), self-grooming (1.03%), and defecating/urinating (0.03%), Figure 5.

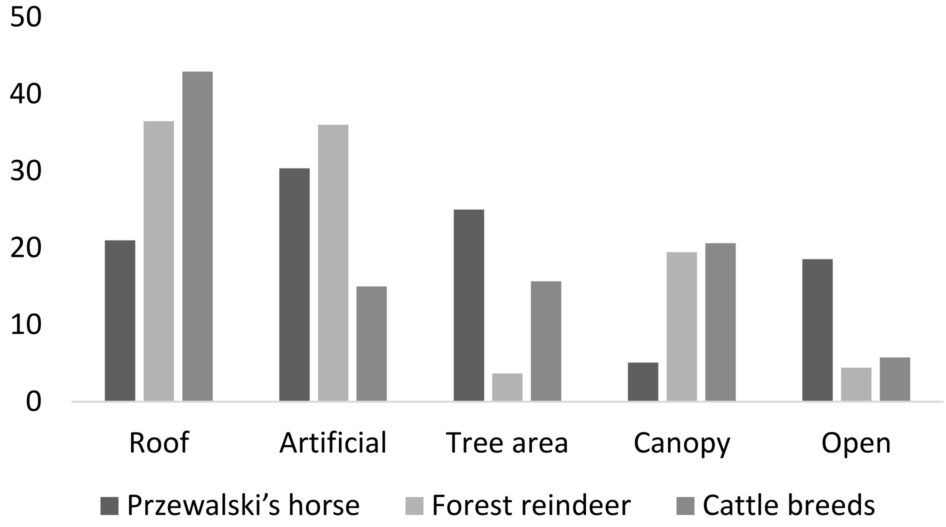

Figure 4. A bar chart illustrating the differences in location utilization (percentage of total time between the years 2019-2024) across five locations for Przewalski’s horses, forest reindeer, and three cattle breeds.

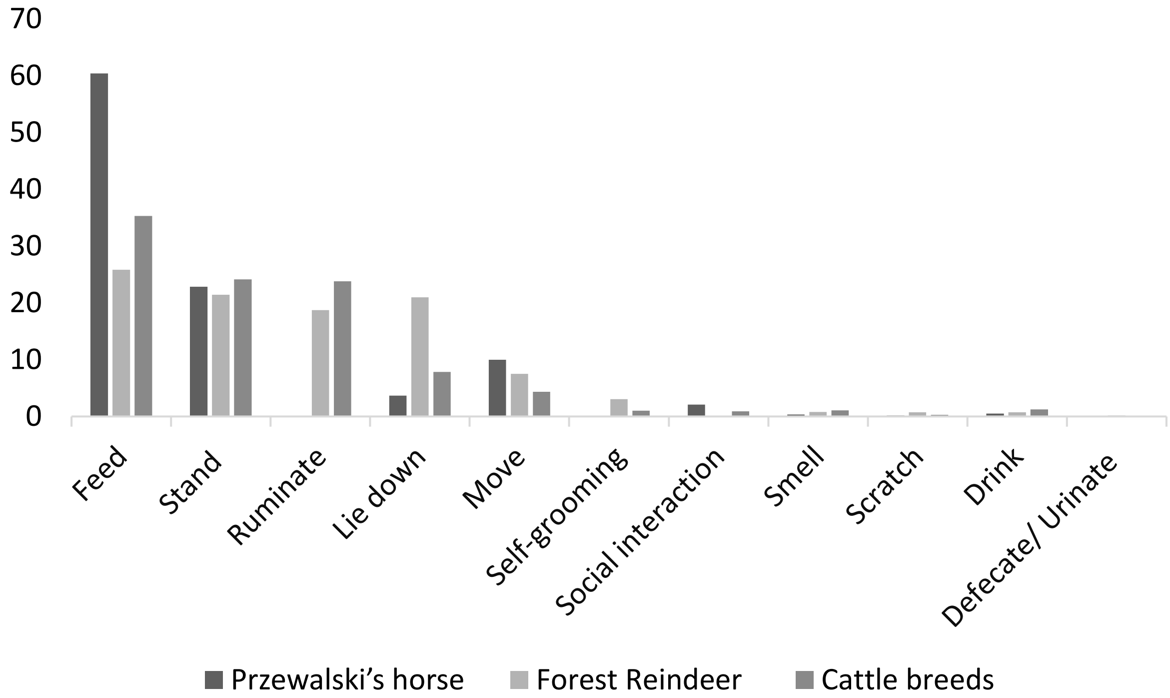

Figure 5. A bar chart illustrating the differences in behaviors performed (percentage of total time between the years 2019-2024) across eleven behaviors for Przewalski’s horses, forest reindeer, and three cattle breeds.

Discussion

The study aimed to investigate how forest reindeer, Przewalski’s horses, and domestic cattle allocate their time across various behaviors and utilize different areas within their enclosures. The goal was to provide insights that could improve enclosure design and animal welfare. The results confirmed the hypothesis that these species exhibit species-specific patterns in spatial use and time allocation for various behaviors. There were also some differences between wild and domesticated animals where cattle spent significantly more time in "artificial" compared to the other species. This supports the idea that domesticated species, such as cattle, may be better adapted to human-managed environments. Cattle also demonstrated a marked preference for "roof" over "open", highlighting their reliance on shelter. The statistical analysis revealed that cattle allocated a significant amount of time to feeding-related behaviors, whereas Przewalski's horses exhibited significantly lower engagement in such behaviors. However, the observational analysis indicated that, relative to other behaviors, feeding-related activities, such as feeding and ruminating in ruminants, accounted for the largest proportion of time in all species.

Forest reindeer, according to the statistical analysis, spent significantly more time in "open" and "tree area" compared to "artificial". However, observational analyses revealed that forest reindeer spent notably less time in "open" (4.41%) and in "tree area" (3.66%) compared to other areas during observations, despite their natural association with forest environments. The observational results suggest that while forest reindeer may naturally prefer these areas, their spatial preferences could be influenced by other factors in their enclosure setup, such as the placement of resources. The positioning of resources, particularly food and water, often placed in artificial areas, could have affected these spatial preferences, as these factors are key drivers of time allocation in captivity.

The differing, and sometimes contradictory, results from the statistical and observational analysis highlight a discrepancy between the aggregated data shown in the graphs and the results from the statistical analyses, which were based on the same dataset but compared at the observation level. The statistical analysis required the use of reference categories, and at times, this led to contradictory results depending on which group was used as the reference. This sometimes makes the statistical results seem less reliable in describing overall patterns. On the other hand, the graphical representations revealed clearer overarching patterns. However, it is important to note that the graphs do not always reflect the underlying variation, which may affect the interpretation of the results.

According to the observational analysis, all species spent a significant amount of time in sheltered areas, such as "roof". This shared tendency to seek shelter can be linked to the animals' need to protect themselves from weather conditions, which is essential for their comfort in captivity (Prince, 1999). All species also spent a lot of time in "artificial" where food was provided and observational comparisons revealed that Przewalski's horses spent the highest proportion of their time feeding (60.40%). Forest reindeer and cattle also spent a considerable amount of time feeding, but less than Przewalski's horses, which can partly be explained by their ruminating behavior, a process that makes up a significant part of their daily activities (18.72% for forest reindeer and 23.78% for cattle).

The statistical analysis showed that cattle spent more time feeding, while Przewalski's horses engaged in more movement and social interactions. When compared to forest reindeer, Przewalski's horses spent more time lying down, moving, and socializing, whereas reindeer allocated more time to feeding and self-grooming. In contrast, the observational analysis revealed that forest reindeer exhibited distinct behavior by spending more time lying down (20.97%) compared to the other species.

The increased time spent lying down by forest reindeer may be related to the fact that ruminants typically rest while lying down. Przewalski's horses spent, according to the observational study, the least amount of time lying down, likely due to their ability to lock the joints in their legs and rest while standing. However, REM sleep can only occur when horses are lying down (Evidensia, n.d.). No animals were observed at night, as observations were conducted during the morning and afternoon, which may influence the behaviors recorded, as they could differ at night.

A similar study by Boyd et al. (1988) investigated the time budgets of a herd of Przewalski's horses in a grass pasture in Front Royal, Virginia, during the summer. The study found that the horses spent 46% of their time feeding, with the highest proportion observed at night (over 60%). This aligns with the findings of the present study, where Przewalski's horses also spent a large portion of their time feeding (60.40%). Differences in percentages may partly be explained by the higher daytime temperatures in Front Royal (28.0°C), which led the horses to prefer grazing during cooler nighttime hours. In the current study at Nordens Ark, horses were fed during the day, and since temperatures were not as high during the observations, they could spend more time feeding when food was available. The Front Royal horses also spent 20.6% of their time standing, 6% lying down, and 7% moving, similar to the results of this observational study, where Przewalski's horses spent 22.85% of their time standing, 9.96% moving, and 3.65% lying down.

In another study by Kilgour et al. (2012), the behavior of six herds of beef steers was observed in Australia during daylight hours to identify what constitutes natural behavior for cattle while grazing. The study was conducted in a manner similar to the observations at Nordens Ark, focusing on studying behaviors under natural conditions with minimal human interference. The results showed that most of the time, over 95%, was spent on four primary activities: grazing, walking, standing while resting/ruminating, and lying while resting/ruminating. Kilgour et al. (2012) also noted that these results are consistent with previous studies examining cattle behavior under similar conditions. These results are consistent with the findings of this observational study conducted at Nordens Ark, where cattle spent 35.32% of their time feeding, 23.78% ruminating, and 24.12% standing.

Comparable patterns are also observed in reindeer. A study by Reimers et al. (2014) on reindeer with both wild and domestic ancestry highlights that, despite certain differences between the two groups, reindeers generally spend most of their time on three main activities: grazing, resting/ruminating, and moving. During the summer and autumn seasons, the time spent grazing is at its peak, reflecting the increased need to build up energy and fat reserves for the winter. During these periods, reindeer spend up to 70% of their time grazing, often in long, continuous periods. Movement between grazing areas is also more frequent during these periods, reflecting the need to utilize high-quality resources. During winter, the time spent grazing decreases in favor of resting and ruminating. This distribution of time across different activities is critical for reindeer's energy and nutritional needs across seasons (Reimers et al., 2014). These findings are similar to those observed in the behavioral study at Nordens Ark, though the reindeer spent more time standing and less time moving. This may be due to the limited space available for movement and the fact that they do not need to search for food.

Understanding animals' time budgets and preferences for specific areas within their enclosures is essential to ensuring their well-being in captivity (Hosey et al., 2009). This study shows that all species spent a significant amount of time feeding, which aligns with findings from the studies mentioned and suggests that the enrichment strategies at Nordens Ark are effective.

Feeding behaviors are essential for animals' well-being and represent an important component of their natural activity patterns (Hosey et al., 2009). These findings underline the importance of enrichment measures, which are a core part of daily care at Nordens Ark. Efforts are informed by how animals live in the wild, their natural behaviors, foraging methods, social structures, and more, with adaptations made accordingly to encourage a variety of behaviors (Nordens Ark., n.d.i).

In summary, the results suggest that factors such as resource placement, enclosure design, and the biological needs of each species may influence animals' behaviors and time budgets. While the specific role of resource placement remains unclear, enriching the environment and designing enclosures that align with animals' preferences appear to have a significant impact. These measures could help improve the animals' overall well-being by encouraging species-specific behaviors and supporting their ecological and psychological needs. Future studies could explore the effect of moving food resources between different locations within enclosures to determine whether this influences habitat use and space utilization. Such insights could further inform optimal enclosure design and resource distribution strategies.

However, there may be an interaction between specific behaviors and the locations in which they are performed, as certain behaviors could be more prevalent in particular areas of the enclosures. This highlights the importance of studying not just overall activity budgets but also the spatial distribution of behaviors to fully understand animals' use of their environments. These observations align with the conclusions of Hosey et al. (2009) and Prince (1999), who stress that understanding animals' behaviors and preferences is crucial for creating optimal captive conditions. That said, it is important to consider that this study was conducted at a single zoological park, with specific enclosures and resource distributions, which may limit the generalizability of the findings to other settings or wild environments.

One of the goals in zoo operations is to contribute to species conservation by preparing animals for reintroduction into the wild. For this to succeed, it is essential that animals maintain natural behaviors and have environments resembling their natural habitats (Hosey et al., 2009; Wark et al., 2019). The findings of this study, which highlight animals' preferences for specific areas within their enclosures, underscore the need to carefully design these environments to facilitate preparations for life in the wild. While increasing movement can be challenging, it can be compensated for by enrichment that encourages animals to spend time on activities other than movement, further supporting their natural behaviors and overall well-being Hosey et al., 2009). Nevertheless, despite the use of standardized protocols during this study, the involvement of multiple observers over several years introduces the potential for variations in how behaviors and space usage were recorded, which could influence the results. Additionally, while the animals were accustomed to the presence of visitors, the presence of observers could still have influenced their behaviors, potentially introducing bias.

Conclusion

This study provides valuable insights into how different species allocate their time to different behaviors and utilize the space within their enclosures. The species-specific and general patterns observed in forest reindeer, Przewalski's horses, and cattle highlight the importance of adapting enclosure designs to address the distinct biological needs of each species. By strategically designing enclosures and carefully considering the placement of key resources, zoos might be able to support species-specific behaviors and enhance animal welfare. These findings suggest that creating environments that align with animals' natural ecological needs could not only benefit their well-being but potentially also contribute to broader conservation goals, such as successful reintroduction into the wild.

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Appendix

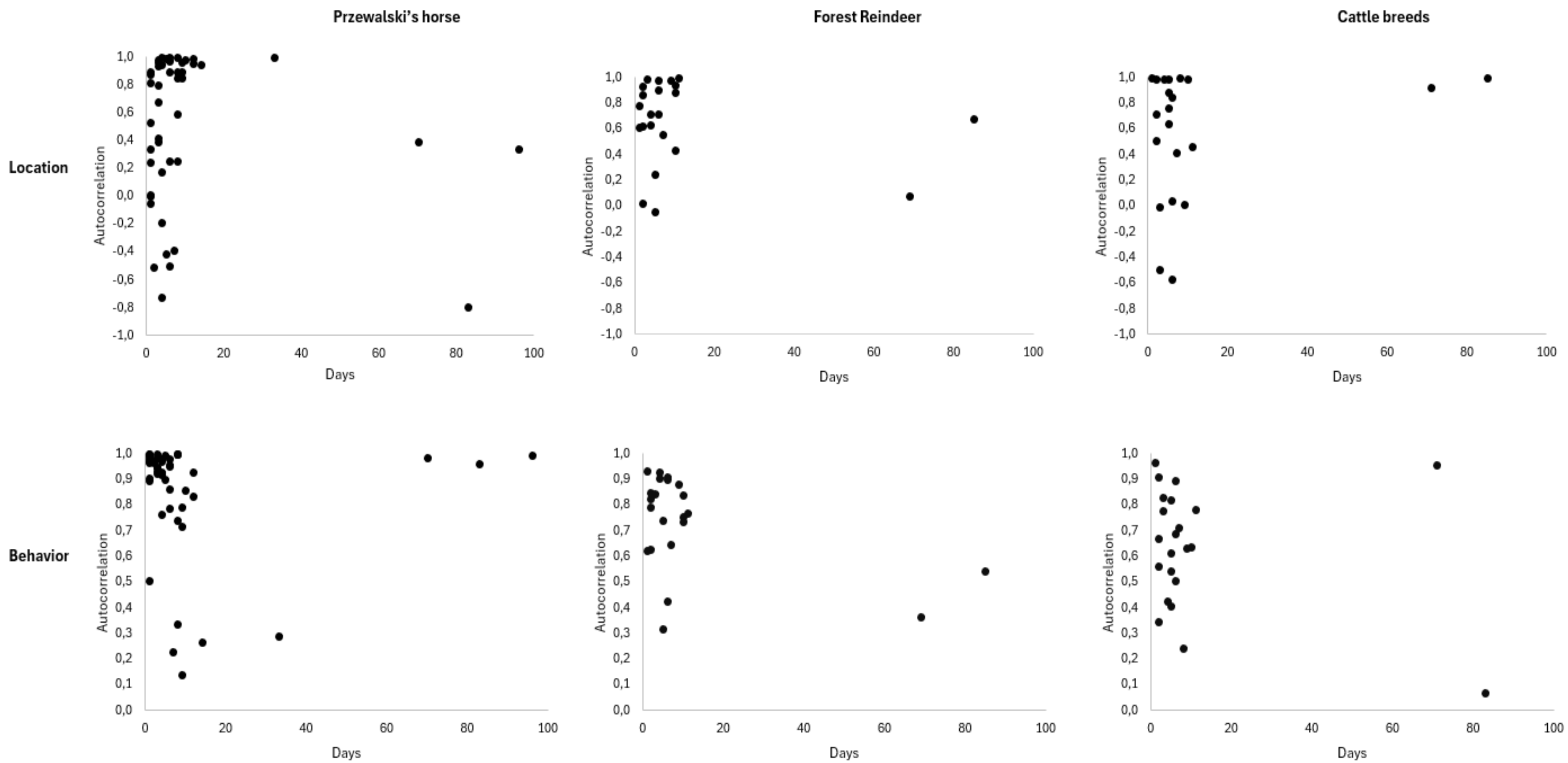

Figure A1. Autocorrelation plots of behavior and location data for horses, reindeer, and cows over 100 days. The y-axis represents days, while the x-axis shows autocorrelation values. Each panel corresponds to species-specific patterns in behavior (left) and location (right), with dots indicating autocorrelation at different time lags.

Table A1. Coefficient estimates (β), standard errors (SE), p-values, AIC, and residual deviance for differences in location use between Przewalski's horses and cattle breeds.

Przewalski's horse vs Cattle breeds					
Location	Coefficient (β)	SE	p-value	AIC	Residual Deviance
Artificial	-393.94	136.43	< 0.001	161.44	141.44
Canopy	514.39	151.58	< 0.001		
Open	-226.68	149.06	0.085		
Roof	272.19	91.20	0.003		
Treearea	-165.97	105.44	0.124		

Table A2. Coefficient estimates (β), standard errors (SE), p-values, AIC, and residual deviance for differences in location use between Przewalski's horses and Forest reindeer.

Przewalski's horse vs Forest reindeer					
Location	Coefficient (β)	SE	p-value	AIC	Residual Deviance
Artificial	-32.47	83.44	< 0.001	161.44	141.44
Canopy	539.79	167.87	0.282		
Open	-147.59	136.56	0.058		
Roof	155.17	81.71	0.016		
Treearea	-514.92	215.52	0.105		

Table A3. Coefficient estimates (β), standard errors (SE), p-values, AIC, and residual deviance for differences in location use between Forest reindeer and cattle breeds.

Forest reindeer vs Cattle breeds					
Location	Coefficient (β)	SE	p-value	AIC	Residual Deviance
Artificial	-350.01	135.93	0.009	161.70	141.70
Canopy	3.32	127.96	0.979		
Open	-36.53	181.48	0.839		
Roof	98.29	87.48	0.262		
Treearea	284.93	201.88	0.148		

Table A4. Pairwise comparisons of location use by Przewalski's horses. Coefficient estimates (β), standard errors (SE), p-values, AIC, and residual deviance are reported.

Przewalski's horse						
Reference Location	Location	Coefficient (β)	Standard Error (SE)	p-value	AIC	Residual Deviance
Artificial	Canopy	-527.0	129.61	< 0.001	784.53	768.53
	Open	-124.83	68.76	0.070		
	Roof	-200.92	75.82	0.008		
	Treearea	-30.75	62.94	0.625		
Canopy	Artificial	424.18	109.02	< 0.001	785.47	769.47
	Open	286.46	111.73	0.010		
	Roof	207.96	115.51	0.072		
	Treearea	398.91	109.2	0.003		
Open	Artificial	170.28	71.42	0.017	784.81	768.81
	Canopy	-331.0	124.43	0.008		
	Roof	-40.0	82.18	0.356		
	Treearea	131.68	72.28	0.068		
Roof	Artificial	220.01	76.65	0.004	784.41	768.41
	Canopy	-339.1	138.24	0.014		
	Open	73.75	81.76	0.367		
	Treearea	179.93	62.97	0.020		
Treearea	Artificial	56.37	62.97	0.371	784.55	768:55
	Canopy	-468.71	125.57	< 0.001		
	Open	-97.84	70.89	0.167		
	Roof	-170.06	77.61	0.028		

Table A5. Pairwise comparisons of location use by Cattle breeds. Coefficient estimates (β), standard errors (SE), p-values, AIC, and residual deviance are reported.

Cattle breeds						
Reference Location	Location	Coefficient (β)	Standard Error (SE)	p-value	AIC	Residual Deviance
Artificial	Canopy	-0.13	0.36	0.714	353.44	337.44
	Open	0.21	0.34	0.540		
	Roof	-0.63	0.40	0.117		
	Treearea	-0.01	0.35	0.974		
Canopy	Artificial	0.09	0.35	0.79	353.58	337.58
	Open	0.29	0.34	0.401		
	Roof	-0.53	0.41	0.191		
	Treearea	0.06	0.36	0.856		
Open	Artificial	-0.16	0.34	0.624	353.61	337.61
	Canopy	-0.35	0.35	0.320		
	Roof	-0.76	0.39	0.051		
	Treearea	-0.22	0.34	0.518		
Roof	Artificial	0.61	0.40	0.125	353.45	337.45
	Canopy	0.46	0.40	0.254		
	Open	0.81	0.39	0.039		
	Treearea	0.59	0.40	0.138		
Treearea	Artificial	0.03	0.35	0.931	353.50	337.50
	Canopy	-0.13	0.36	0.715		
	Open	0.21	0.34	0.525		
	Roof	-0.58	0.40	0.149		

Table A6. Pairwise comparisons of location use by Forest reindeer. Coefficient estimates (β), standard errors (SE), p-values, AIC, and residual deviance are reported.

Forest reindeer						
Reference Location	Location	Coefficient (β)	Standard Error (SE)	p-value	AIC	Residual Deviance
Artificial	Canopy	0.69	0.44	0.118	355.24	339.24
	Open	1.26	0.43	0.003		
	Roof	-0.04	0.48	0.936		
	Treearea	1.32	0.43	0.002		
Canopy	Artificial	-0.73	0.43	0.092	355.58	339.58
	Open	0.47	0.36	0.190		
	Roof	-0.84	0.45	0.059		
	Treearea	0.53	0.36	0.133		
Open	Artificial	-1.14	0.43	0.008	356.21	340.21
	Canopy	-0.42	0.36	0.249		
	Roof	-1.12	0.43	0.009		
	Treearea	0.22	0.33	0.508		
Roof	Artificial	-0.08	0.45	0.866	357.56	341.56
	Canopy	0.42	0.42	0.319		
	Open	0.97	0.40	0.017		
	Treearea	1.02	0.40	0.011		
Treearea	Artificial	-1.14	0.42	0.007	357.34	341.34
	Canopy	-0.41	0.36	0.249		
	Open	0.012	0.33	0.720		
	Roof	-1.20	0.43	0.005		

Table A7. Behavioral differences between cattle breeds and Przewalski's horses. Coefficient estimates (β), standard errors (SE), p-values, AIC, and residual deviance are presented.

Cattle breeds vs Przewalski's horse					
Behavior	Coefficient (β)	Standard Error (SE)	p-value	AIC	Residual Deviance
Defecate/ Urinate	0.69	1.61	0.904	1974.34	1886.34
Drink	-0.27	0.25	0.520		
Feed	0.27	0.10	0.027		
Lie down	-0.20	0.11	0.172		
Move	-0.40	0.09	0.000		
Scratch	0.13	0.24	0.849		
Self-grooming	0.207	0.15	0.349		
Smell	-0.28	0.18	0.270		
Social interaction	-0.88	0.15	<.0001		
Stand	-0.3258	0.1040	0.009		

Table A8. Behavioral differences between Przewalski's horses and Forest reindeer. Coefficient estimates (β), standard errors (SE), p-values, AIC, and residual deviance are presented.

Przewalski's horse vs Forest reindeer					
Behavior	Coefficient (β)	Standard Error (SE)	p-value	AIC	Residual Deviance
Defecate/ Urinate	-0.27	1.55	0.984	1974.34	1886.34
Drink	0.18	0.25	0.759		
Feed	-0.61	0.12	<.0001		
Lie down	0.28	0.10	0.026		
Move	0.30	0.09	0.007		
Scratch	-0.87	0.24	0.002		
Self-grooming	-0.79	0.15	<.0001		
Smell	0.30	0.19	0.284		
Social interaction	0.94	0.08	<.0001		
Stand	0.29	0.11	0.029		

Table A9. Behavioral differences between cattle breeds and Forest reindeer. Coefficient estimates (β), standard errors (SE), p-values, AIC, and residual deviance are presented.

Cattle breeds vs Forest reindeer					
Behavior	Coefficient (β)	Standard Error (SE)	p-value	AIC	Residual Deviance
Defecate/ Urinate	0.42	3.15	0.990	1974.34	1886.34
Drink	-0.09	0.21	0.902		
Feed	-0.34	0.20	0.232		
Lie down	0.08	0.09	0.631		
Move	-0.10	0.08	0.446		
Ruminate	-0.23	0.20	0.491		
Scratch	0.74	0.48	0.288		
Self-grooming	-0.59	0.30	0.127		
Smell	0.01	0.16	0.996		
Social interaction	0.06	0.08	0.707		
Stand	-0.04	0.09	0.915		