Triggers and treatments for pacing in the Carpathian Lynx (*Lynx lynx carpathicus*)

A behavioural study at Borås Zoo

Linnéa Boije

Independent project • 30 credits
Swedish University of Agricultural Sciences, SLU
Department of Applied Animal Science and Welfare
Animal Science – Master's programme
Uppsala 2026

Triggers and Treatments for Pacing in the Carpathian Lynx (*Lynx lynx carpathicus*)

A Behavioural Study at Borås Zoo

Linnéa Boije

Supervisor:	**Lisa Lundin, Swedish University of Agriculture Science, Department of Applied Animal Science and Welfare**
Examiner:	Josefina Zidar, Swedish University of Agriculture Science, Department of Applied Animal Science and Welfare

Credits:	30 credits
Level:	A2E
Course title:	Independent project in Animal Science
Course code:	EX0870
Programme/education:	Animal Science – Master's programme
Course coordinating dept:	Department of Applied Animal Science and Welfare
Place of publication:	Uppsala
Year of publication:	2026
Cover picture:	Linnéa Boije
Copyright:	All featured images are used with permission from the copyright owner.
Keywords:	Carpathian Lynx, triggers, pacing, enrichment, conservation

Swedish University of Agricultural Sciences

Faculty of Veterinary Medicine and Animal Science

Department of Applied Animal Science and Welfare

Abstract

Conservation work is an important part in preserving biodiversity. *Ex situ* conservation at zoos is today an essential part to preserve healthy population sizes and to gain interest in the subject from the public. For wild animals, captivity can be a stressful environment that induces stereotypic behaviours such as pacing. At Borås Zoo, two Carpathian lynxes (*Lynx lynx carpathicus*) are housed where the female has developed pacing as part of her behavioural repertoire. To improve welfare and reduce stereotypic behaviour an evaluation if activity in proximity to the enclosure induces pacing, and if different foraging enrichments reduce the stereotypic behaviour, was performed. The study included a control period with regular routines and three treatments where feed was provided based on natural foraging behaviour of wild lynx. Treatment 1 had a winch which was lowered at specific times and provided feed. Treatment 2 included full-carcass feeding of a roe deer carcass. Treatment 3 included the winch with a setting that lowered and raised the feed multiple times. The analysis of activity in proximity showed a correlation between keepers' activity, cars, tractors and the prevalence of pacing. The feeding enrichments had an impact on the occurrence of pacing, reducing both frequency and duration of the behaviour in all treatments. The results indicate that well adapted enrichment for Carpathian Lynxes in captivity can help improve welfare by reducing stress from the environment.

Keywords: Carpathian Lynx, triggers, pacing, enrichment, conservation

Table of contents

1. Introduction **7**
1.1 Lynx Lynx 7
1.2 The difficulty in captivity for wild animals 8
1.3 Stereotypic behaviour 9
1.4 The visitor effect 10
1.5 Legislation in Sweden 10

2. Aim **12**
2.1 Questions: 12

3. Material and method **13**
3.1 Location and study site 13
3.2 Individuals 14
3.3 Data collection 14
3.4 Ethogram 15
3.5 Control and treatments 17
3.6 Data analysis 18

4. Results **20**
4.1 Behavioural diversity 20
4.2 Behaviour repertoire 22
4.3 Pacing 24
4.4 Activity in proximity 26

5. Discussion **28**
5.1 Behavioural diversity 28
5.2 Behaviour repertoire 28
5.3 Pacing 30
5.4 Activity in proximity 31
5.5 Treatment design 32
5.6 Reflections on method 33
5.7 Limitations of the study 34
5.8 Social and sustainability aspects 36
5.9 Ethical aspects 37

6. Conclusion **39**

7. Thank you **40**

References **41**

Popular science summary **47**

1. Introduction

1.1 Lynx Lynx

The Carpathian Lynx (*Lynx lynx carpathicus*) is a geographic subspecies of the Eurasian Lynx (*Lynx lynx*) (Borås Djurpark n.d.). The lynx belongs to the family *Felidae* (Svenska Rovdjursföreningen, n.d.). The population of the Eurasian lynx is considered of least concern according to the IUCN Red List (Breitenmoser et al. 2025). Earlier, hunting for fur and diseases have had a negative effect on the Eurasian lynx population size, but due to successful conservation work the population has had a gradual increase (Borås Djurpark n.d.; Nordens Ark n.d.). As part of ex-situ conservation work by EAZA (European Association of Zoos and Aquaria) for the Eurasian lynx, the Carpathian lynx is housed at Borås Zoo (Borås Djurpark n.d; EAZA 2025).

In the wild the lynx lives in forests, shrubland, grassland and rocky areas (Breitenmoser et al. 2025). They switch between habitats depending on daytime and nighttime and often adapt their movement to get further from human activity (Filla et al. 2017). During daytime they prefer coniferous forests and often move toward higher altitudes while during nighttime they are driven by prey to more deciduous forests and meadows on a lower altitude. In the wild they hunt herbivores as large as roe deer (*Capreolus capreolus*) but also smaller prey such as hares (*Lepus*) (Filla et al. 2017; Svenska Rovdjursföreningen n.d.). Wild lynx refrain from eating carcasses compared to many other carnivores (Svenska Rovdjursföreningen n.d.). Their circadian rhythm corresponds with the crepuscular activity pattern of their main prey, the roe deer (Heurich et al. 2014). Their activity is therefore very dependent on light conditions, and their activity patterns peak during twilight (Heurich et al. 2014; Fila et al. 2017).

The adult lynx is a solitary animal and only interacts with other lynxes during mating season or when the female has cubs (Svenska Rovdjursföreningen n.d.). The cubs live with their mother for approximately a year. Lynxes live in large territories (males approximately 400 km^2; females approximately 120 km^2**)** with a variety of nature types ranging from coniferous forests to meadows (Filla et al. 2017; Nordens Ark n.d.). A male lynx territory often overlaps one to two females home ranges, which the male attempts to monopolise from other males (Vogt et al. 2014). During mating season communication with other lynxes increases, both through scent marking and vocalisation (Svenska Rovdjursföreningen n.d; Vogt et al. 2014). Scent marking is increased especially in marking sites, which are smaller areas that have a high chance of conspecifics visiting (Gosling & Roberts 2001). These marking sites are used to protect a territory and inform other lynxes of their presence; therefore, it is increased during mating season for a higher probability of attracting females (Vogt et al. 2014). It has been shown that the females often scent-mark on top of the resident males, but the reason is unknown (Vogt et al. 2014). During mating season, the males sometimes leave their home range to novel habitats for mate-searching, and these marking sites help them navigate in ownership relations and probability of finding females (Vogt et al. 2014; Liang et al. 2026).

1.2 The difficulty in captivity for wild animals

Wild animals kept in captivity are exposed to new challenges in the captive environment compared to challenges in the wild which can lead to high levels of stress (Morgan & Tromborg 2007).

Following an animal's circadian rhythm can be difficult with captive animals. As mentioned above, the lynx follows a crepuscular circadian pattern and hunts during dusk and dawn (Fila et al. 2017), compared to us humans who have an endogenous circadian rhythm (Hofstra & de Weerd 2008). This results in interactions between keepers and animals to occur during hours that conflict with the lynx's activity pattern. Studies on cheetahs (*Acinonyx jubatus*) and lions (*Panthera leo*) in captivity show that they can adapt to the animal keepers' routines without too much disruption of their circadian rhythm (Seyrling et al. 2022). However, this is not proven in lynxes. In other animal models such as small rodents, it has been shown that a disruption from the natural circadian rhythm can induce stress and depression (Walker et al. 2020). To reduce the negative effects of disruptive circadian rhythm, such as chronic stress, exercise and enrichment has been proven effective in mammals (Solberg et al. 1999). Providing enrichment can therefore reduce stereotypic behaviours, such as pacing, that originate from the stress in captive environments.

In the wild, animals communicate with conspecifics and with other species through scent marking (Vogt et al. 2014; Cornhill & Kerley 2020). In other felids in the wild it has been proven that they might refrain from scent-marking and marking sites if a larger predator has marked the area before them (Cornhill & Kerley 2020; Allen et al. 2023). It has also been observed that olfactory communication increases with the absence of large predators in the Pallas's cat (*Otocolobus manul*) (Allen et al. 2020). If larger carnivores influence lynx behaviour, in either the wild or captivity, is not yet explored. However, since the behaviour has been observed in other smaller carnivores it is probable that large predators can impact lynxes' behaviour and welfare in captivity where they cannot avoid proximity to each other.

Conserving an animal's natural behaviours and behavioural diversity can be difficult in captive environments (Rabin 2003). Behavioural diversity is something that can indicate the animal's welfare (Miller et al. 2020). Behavioural diversity is the number and frequency of behaviours an animal performs (Miller et al. 2020). The assumption is that when behavioural diversity is high the animals' behavioural needs are better fulfilled and when the diversity is low it may show poor welfare (Miller et al. 2020). However, to use this as an indication of the animal's welfare demands a deep knowledge of the animal's range of natural behaviours in the wild which can be difficult due knowledge gaps in certain species. Another challenge with using behavioural diversity could be knowing where to draw the line between high and low behavioural diversity, thus making it difficult to interpret if an animals behavioural diversity indicates a good or bad welfare. Behavioural diversity as a welfare indicator should therefore be used with caution and paired with other indicators (Watters et al. 2021).

1.3 Stereotypic behaviour

If the captive environment is not adapted to the animals' natural behaviours an increase in stress and stereotypic behaviours has been shown in felids (Marinath et al. 2019). Stereotypic behaviour can be explained with repetitive, unvarying sequences of locomotion that lacks function (Ödberg 1987). This means that stereotypic behaviour can indicate that a change in environment is needed to improve welfare.

There are different ways to tackle stereotypic behaviour, the most common way is environmental enrichment (Mason et al. 2007). A meta-analysis showed that enrichment has a significant effect on stereotypy performance and has reduced the problematic behaviour in 53% of times in reviewed research (Swaisgood & Shepherdson 2005). But for enrichment to have a positive effect it needs to be adapted to the animal's natural behaviour, be biologically relevant and that the animals engage with the enrichment (Skibiel et al. 2007). There can also be species specific as well as individual differences in preference and effect of enrichment (Damasceno et al. 2017). For zookeepers it can be difficult to find well adapted enrichment for their animals and to have time to evaluate them (Tuite et al. 2022).

Pacing

A common stereotypic behaviour in captive felids is pacing (Lyons et al. 1997; Clubb & Mason 2003; Meredith et al. 2007; Burgener et al. 2008). Pacing is a locomotory stereotypic behaviour where the animal walks back and forth, in circles or in the figure of an eight (Clubb & Vickery 2006). There are several hypotheses as to why pacing is so frequent in captive carnivores, a widespread explanation is frustration from not being able to perform natural behaviours such as hunting (Clubb & Vickery 2006). The locomotion of pacing may serve as replacement behaviour of the search phase during a hunt. Providing enrichment that stimulates natural hunting behaviour can be difficult (Mason et al. 2007). Another suggestion is that pacing originates from restricting the animals' natural ranging behaviour when kept in captivity (Clubb & Mason 2007). If the species have a large home range in the wild, they more often develop pacing. A third hypothesis is that the stress from 'the visitor effect' can induce stereotypic behaviour, such as pacing (Swaisgood & Shepherdson 2006).

1.4 The visitor effect

When keeping wild animals in captivity, such as zoos, the proximity to people increases markedly (Davey 2007). The 'visitor effect' is the concept of how the animals kept in captivity are affected by the proximity of humans in a captive environment. This can have both a positive and negative effect on the welfare of captive animals, some animals experience stress from visitors while for others it becomes enriching (Davey 2007). Suárez et al. (2017) studied different large felids in zoo environments. Lynxes, bobcats and ocelots reduce their activity levels when visitors are present which was supported by Spiezio et al. (2023). In the study by Suárez et al (2017) there was also an increase in agonistic behaviour in the lynxes when the zoo was open. However, for the jaguar in the same study an increase in positive behaviours was seen, such as playing and exploring, which supports the claim that the visitor effect can be enriching. However, this does not have to be linked to certain species but instead individual differences such as personality and former experiences (Davey 2007; Suárez et al 2017). To lessen the impact visitors have on animals, habituation with visitors can be important for certain individuals and the opposite for others, for whom breaks from an audience is the most important (Hosey 2000).

The visitor effect can also impact enclosure utilisation, many large felids often prefer hiding and retreat spaces instead of open areas when the zoo is open (Suárez et al. 2017). This can be a way of coping with the stress from visitors by trying to escape from their view. The design of the enclosure determines the animals' possibility to remove themselves from visitor view and can therefore, have a large impact on the visitor effect (Hosey 2000). An enclosure that is adapted to the animals wants and needs can decrease the negative effect of visitors (Davey 2007).

1.5 Legislation in Sweden

In Sweden animals kept in zoos are protected by the Animal Welfare Act (SFS 2018:1192), the Animal Welfare Ordinance (SFS 2019:66) and the Swedish Board of Agriculture's regulations and general advice on animal keeping in zoo's (SJVFS 2019:29).

It is illegal to use live animals as feed due to the Animal Welfare Act (SFS 2018:1192), which states that all animals must be treated well and protected from unnecessary suffering and disease. The legislation requires that animals be kept in a suitable environment that promotes their welfare, encourages natural behaviour and prevents abnormal behaviour (SFS 2018:1192). This is further stated in SJVFS:2019:29, the animal enclosure needs to be adapted to the species and enriched in such a way that the animals are able to behave naturally. The enrichment can be in the enclosures' design as well as daily maintenance. The regulations (SJVFS:2019:29) state that the enclosures need to be designed to prevent that animals in adjacent enclosures hurt or induce stress and that the animals can be inspected without being subjected to unnecessary stress. The regulations also state that the enclosure must have one side that functions as privacy protection or that the enclosure design achieves an equivalent effect.

2. Aim

Pacing is a frequent problem in carnivores, especially in large felids (Clubb & Mason 2003; Meredith et al. 2007; Burgener et al. 2008; Cambrelen & Slater 2023). For lynxes, triggers and treatments for this are unknown due to lack of scientific research in lynx behaviour in both captivity and the wild, which calls for further research in the area. At Borås Zoo, pacing is a concerning problem for the Carpathian lynxes, specifically the female.

The aim of this project is to explore environmental triggers that increase pacing in captive Carpathian Lynx (*Lynx lynx carphaticus*) at Borås zoo. The thesis also aims to explore the effect of three different enrichments on lynxes' behaviour and evaluate if biologically relevant enrichment can reduce stereotypic pacing.

2.1 Questions:

- How does feeding enrichment designed to reflect the lynx's natural foraging influence their behaviour?
- Does feeding enrichment adapted to the lynx's natural behavioural needs reduce pacing?
- Does activity in proximity to the enclosure trigger pacing in the Carpathian lynx and if so, which activities?

3. Material and method

3.1 Location and study site

The observations were conducted at Borås Zoo in Sweden through cameras placed in the lynx enclosure. The enclosure was divided into three parts with free access through small open gates between them with a total area of 2902.2 m^2. Two parts of the enclosure could be viewed from the visitor walkway and there was a back enclosure non-viewable for visitors. In the back enclosure, there was an indoor area of 12 m^2. The enclosure consisted of mainly coniferous forest with some small open areas at the back, furthest away from the visitor walkway. There were two artificial lairs, one placed in the back enclosure and one in the largest. Behind the enclosure the coniferous forest continued. On the other side of the visitor walkway the brown bear (*Ursus arctos*) enclosure was located, and European bison (*Bison bonasus*) were located next to the back enclosure. The cameras used for observation were positioned in the back of each enclosure section (Fig. 1). The cameras were installed previously by the zoo, so placement of cameras was not decided with this study in consideration. The cameras placement provided an overview of the majority of the enclosure. When nighttime came a light was automatically activated on the cameras.

Figure 1. A satellite photo of the lynx enclosure at Borås Zoo. The red dots show the approximate placing of the cameras.

3.2 Individuals

Two Carpathian lynx (*Lynx lynx carpathicus*) were observed in this study. A breeding pair consisting of an eight-year-old female and a three-year-old male. They had lived at Borås Zoo for approximately one and half years. The female had performed pacing before the study, while the behaviour had not previously been recorded in the male.

3.3 Data collection

The observations were performed during a twelve-week period from the 26th of January to the 19th of April 2026. The park was closed for visitors during the observations except between 3/4-6/4 and 9/4-11/4 when the park was open between 10.00-16.00. The study period was divided into four parts, each part three weeks long. During part one and three the observations were conducted Monday to Friday and during part two and four they were conducted Monday to Saturday. Each observation day consisted of three periods of data collection, at 04.00-06.00, 08.00-10.00 and 12.00-14.00. The time for observations were determined based on the results of a pilot study and lynxes' circadian rhythm. The observations were performed using video recording from the cameras in the program NX Witness Client.

The data that was collected was behavioural data and different activities in proximity to the enclosure. This was collected throughout the observation period. The program used for behavioural data was ZooMonitor (version 4.1). Behaviours described in an ethogram was collected using continuous focal sampling, both duration and frequency of the behaviours were recorded, however only duration was later used in the analysis. The behavioural data from both individuals was then combined to represent the behavioural activity as a group. Activity in proximity to the enclosure was recorded through ad libitum sampling during the observation periods to minimise the risk of missing potential triggers. Any visible movement from vehicles, humans or animals near the lynxes and if routines were changed were noted as activity. This was observed through video recordings and communication with the keepers through e-mail and text message when activities occurred.

3.4 Ethogram

For the behavioural data collection an ethogram was constructed (Tab. 1). A pre-existing ethogram made by Stanton et al. (2015) for felids was used as the base and then the behaviours that were deemed valuable for the aim of this study and thought to be possible to observe in the video recording were included. The ethogram by Stanton et al. (2015) was used as framework to ensure consistency in behavioural classification. Behaviours relevant to the aims of the present stud and considered observable from the video recordings were selected and included in the final ethogram. The description of some behaviours from the original ethogram was changed and a few behaviours were combined which can be seen in italics (Tab. 1).

Table 1. Ethogram based on Stanton et al. (2015) that was used during observations.

Behaviour categories	**Behaviour**	**Definition**
Inactive	Sitting	Lynx is in an upright position, with the hind legs flexed and resting on the ground, while front legs are extended and straight.
	Lying	Lynx's body is on the ground in a horizontal position, including on its side, back, belly, or curled in a circular formation.
	Sleeping	Lynx is lying on the ground or object with its head down and eyes closed, performing minimal head or leg movement..
Active	Standing	Lynx is in an upright position and immobile, with all four paws on the ground and legs extended, supporting the body.
	Stretching	Lynx extends its forelegs or hind legs while sometimes curving its back inwards.
	Treading	Rhythmic, raising and lowering of paws so that the lynx is stepping in place.
	Walking	Forward locomotion at a slow gait.
	Running	Forward locomotion in a rapid gait, which is faster than walking or trotting.
	Jumping	Lynx leaps from one point to another, either vertically or horizontally.
	Climb	Lynx ascends and/or descends an object or structure.
	Explore	Lynx moves around attentively while smelling by inhaling air through the nose on the ground and/or objects.

	Eat	Lynx ingests edible substances by means of chewing with the teeth and swallowing.
	Flinch	Lynx approaches and/or sniffs an object or other lynx, but abruptly stops and retreats or flees from it.
	Rear	Lynx stands up on its hind legs with forelegs toward or against an object.
	Roll	While lying on the ground or other object, lynx rotates body from one side to another. During the roll, the back is rubbed against ground, the belly is exposed, and all paws are in the air. Lynx may continue rolling repeatedly from side to side.
	Body rub	Lynx rubs any part or entire length of body against an object.
	Groom	Lynx cleans itself by licking, scratching, biting or chewing the fur on its body. May also include the licking of a front paw and wiping it over one's head.
	Manipulate object	Lynx uses any part of body to touch, hold, move or pick up an object.
	Scratching	Lynx scratches its body using the claws of its hind feet.
	Kneading	Lynx pushes forepaws into the ground or objects in a rhythmic, kneading motion.
	Urinate	Lynx releases urine in the ground while in a squatting position.
Stereotypic behaviour	Pacing	Repetitive locomotion in a fixed pattern, such as back and forth along the same route. Can include walking, trotting and running. Movement seems to have no apparent goal or function. Must be performed at least two times in a succession before qualifying as stereotypic.
Social behaviour	Urine spray	While standing with tail raised vertically, lynx releases a jet of urine backwards against a vertical surface object.
	Follow	Lynx travels closely behind other lynx.
	Attack	Lynx launches itself at other lynx with extended forelegs and attempts to engage in physical combat.

	Huddling	Lynx is at rest, lying or sitting with body in contact with another lynx.
	Flee	Lynx runs away from other lynx.
	Playing	Lynx interacts with something in a “non-serious” manner (i.e. where there is no *apparent* intention of harm).
	Stalk	Slow, forward locomotion in a crouched position directed towards another lynx, with head kept low and eyes focused on said lynx.
	Chase	Lynx runs rapidly in pursuit of another lynx.
	Wrestle	Lynx engages in physical contact with another lynx, whereby the lynx struggles with other individual. Both individuals are participating in the physical contact and struggles with the other lynx. Can include pulling towards itself with its forelegs and perform raking movements with the hind legs.
Not visible	Not visible	Lynx is not visible or it is difficult to determine what the lynx is doing due to vision hinderance for the observer.

3.5 Control and treatments

Control

During the first three weeks of the observation period regular routines were followed and only familiar enrichment was provided.

Treatment 1

In treatment 1 a winch, that was novel to the lynxes, was installed in the middle of the back enclosure visible for camera footage. A horse leg was attached to the winch and the winch raised up in the air making it unattainable for the lynxes the day before lowering. The feed was not possible to remove from the winch for the lynxes. At 05.30 on specific dates the winch lowered the feed and stayed down until the lynxes had eaten it all or it turned bad in which case it was removed by keepers. This was repeated five times during part two according to a pre-determined schedule (Tab. 2).

Treatment 2

Treatment 2 was also a novel enrichment for these lynxes. A full body roe deer was provided at the start of each week (Tab. 2). The feed was chained to a tree in view of a camera at the back of the middle enclosure to ensure that it was not moved to a non-visible location. When the lynxes had finished the roe deer the keepers removed the remains.

Treatment 3

In treatment 3 the winch was used again but with other timing settings. As in treatment 1 a horse leg was attached to the winch which was not attainable for the lynxes in the raised position. The winch was lowered five times each enrichment date and was raised again after 2.5 minutes except the last time when it stayed down (Table 2). The times when it was lowered was 20.00, 22.30, 02.30, 05.00 and lastly 06.00. The feed during this part was possible for the lynxes to remove when in the lowered position.

Table 2. Schedule for enrichments for the whole study, enrichments during treatments was only provided on Mondays and Thursdays.

Week of observation period	Treatment	Monday	Thursday
1	Control	Regular routines	Regular routines
2	Control	Regular routines	Regular routines
3	Control	Regular routines	Regular routines
4	Treatment 1 – Winch	16/2	19/2
5	Treatment 1 – Winch	23/2	26/2
6	Treatment 1 – Winch	2/3	
7	Treatment 2 – Full body feed	9/3	
8	Treatment 2 – Full body feed	16/3	
9	Treatment 2 – Full body feed	23/3	
10	Treatment 3 – Moving winch	30/3	2/3
11	Treatment 3 – Moving winch	6/4	9/4
12	Treatment 3 – Moving winch	13/4	16/4

3.6 Data analysis

The collected data was downloaded from ZooMonitor and the raw data was processed in Microsoft Excel.. The frequencies and duration of all behaviours during each observation period were converted to proportion of time spent performing that behaviour and then compiled into diagrams. The behavioural categories were then compiled, and proportion of each category was calculated. For the behavioural data of pacing, descriptive statistics including means and standard errors were calculated to summarise data and comparisons of treatments. Descriptive statistics were chosen due to the small sample size. The proportion of time spent pacing over each observation treatment was compiled for comparison. For activity in proximity the ad libitum data was converted into one-zero data-collection, if activity happened during an observation, it was marked as one. The data was transferred to SPSS version 32. A negative binomial regression analysis was performed to model the relationship between the predictor variables, activities in proximity, and the count outcome variable, pacing. Negative binomial regression was chosen instead of Poisson regression due to overdispersion in the data (variance greater than the mean).

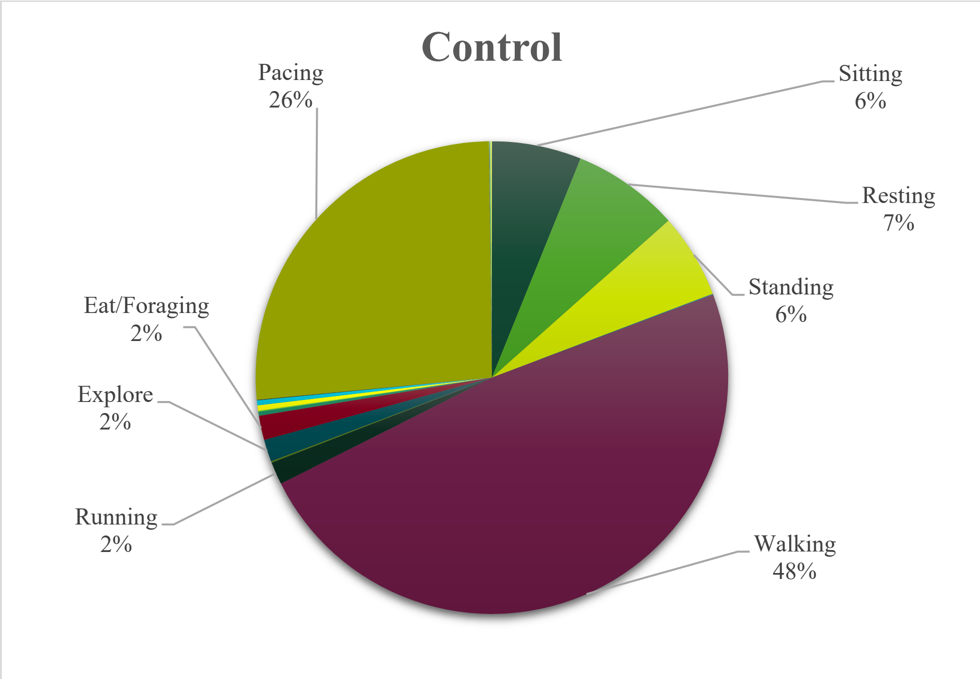
4. Results

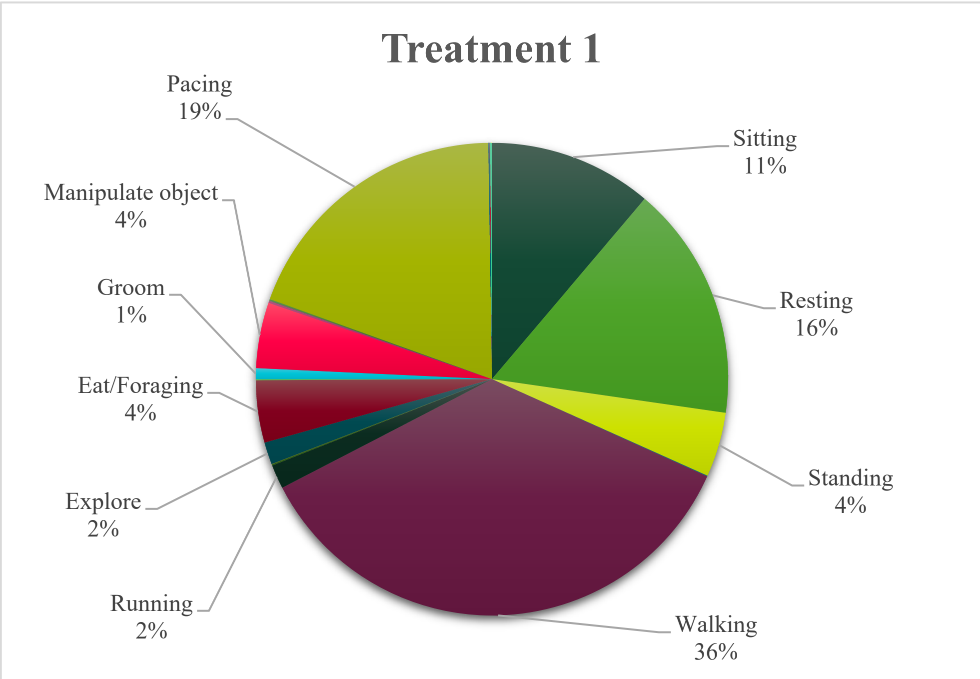
A total of 66 days of observation were included in the study, with 15 days each for control and treatment 2 and 18 days each for treatment 1 and 3. During Treatment 3 there were technical problems with the winch due to a storm on the 6th of April which resulted in the enrichment not being presented on that date as planned.

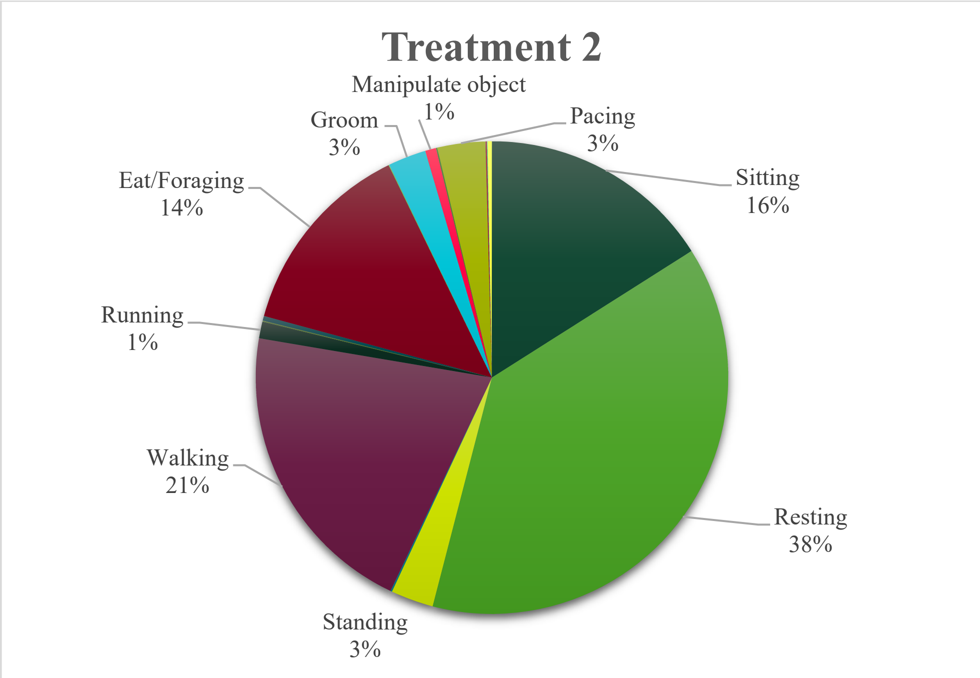
Pacing was only observed in the female lynx and never in the male, the rest of the behaviours were performed by both individuals. Rear, chase and wrestle were never observed and have therefore been removed from analysis. In

4.1 Behavioural diversity

The behavioural diversity broadened in all treatments compared to control (Fig. 2). The range of behaviours increased, and the behaviours were more evenly distributed when the novel enrichments were provided in contrast to the control period (Fig. 2). In control eight behaviours had a percentage of time ≤1%. In Treatment 1 and 3 ten behaviours was performed ≤1% of time. Treatment 2 nine behaviours were performed ≤1% of time. During the treatments, the difference in proportion of time for behaviours such as resting, sitting, walking became more evenly distributed while pacing decreased (Fig. 2). In control eating/foraging was below 1% compared to in the treatments where it was at least above 4%.


Control
Pacing
26%
Sitting
6%
Resting
7%
Standing
6%
Eat/Foraging
2%
Explore
2%
Running
2%
Walking
48%


Treatment 1
Pacing
19%
Sitting
11%
Manipulate object
4%
Groom
1%
Resting
16%
Eat/Foraging
4%
Standing
4%
Explore
2%
Running
2%
Walking
36%



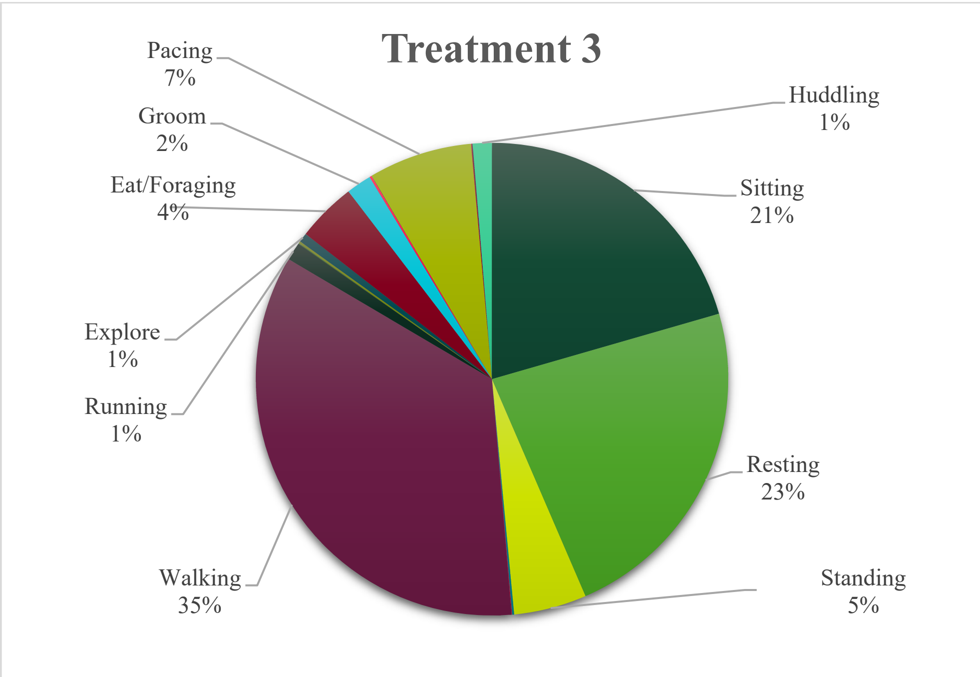


Figure 2. The proportion of behaviours observed in each observation period to present behavioural diversity. Not visible is not included.

4.2 Behaviour repertoire

The most common behaviour in both individuals was ‘not visible’ during the whole study (Fig. 3). A decrease in time spent ‘not visible’ was seen in treatment 1 and 2 compared to control while during treatment 3 there was an increase (Fig. 3). A decrease in stereotypic behaviour was seen in all treatments, with a decline through each treatment (Fig. 3). Social behaviours were low in both frequency and duration and were only observed 0.08% of time during the whole study. Due to the low occurrence of social behaviours, they were combined and analysed in its category during processing of the raw data.

In treatment 2 'Eating/Foraging' was performed in a higher proportion of time compared to other observation periods (Fig. 4). 'Grooming' and 'Inactive behaviour' was also performed more in treatment 2 compared to other treatments and control (Fig. 4).

Pacing was the most common during 08.00-10.00 compared with other observation times (Fig. 5).

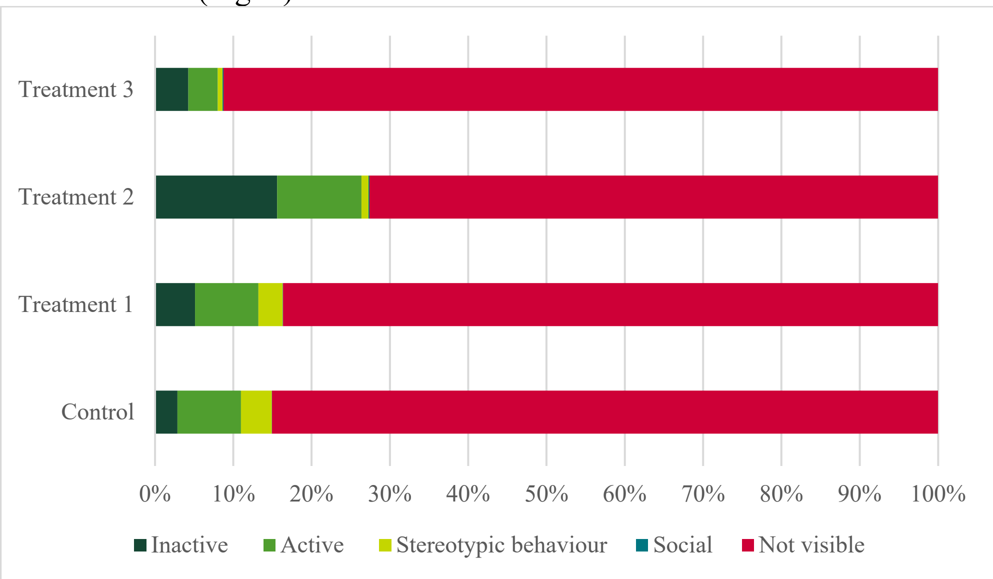


Figure 3. The percentage of time each behaviour category in the ethogram (Tab. 1) was observed in each observation period.

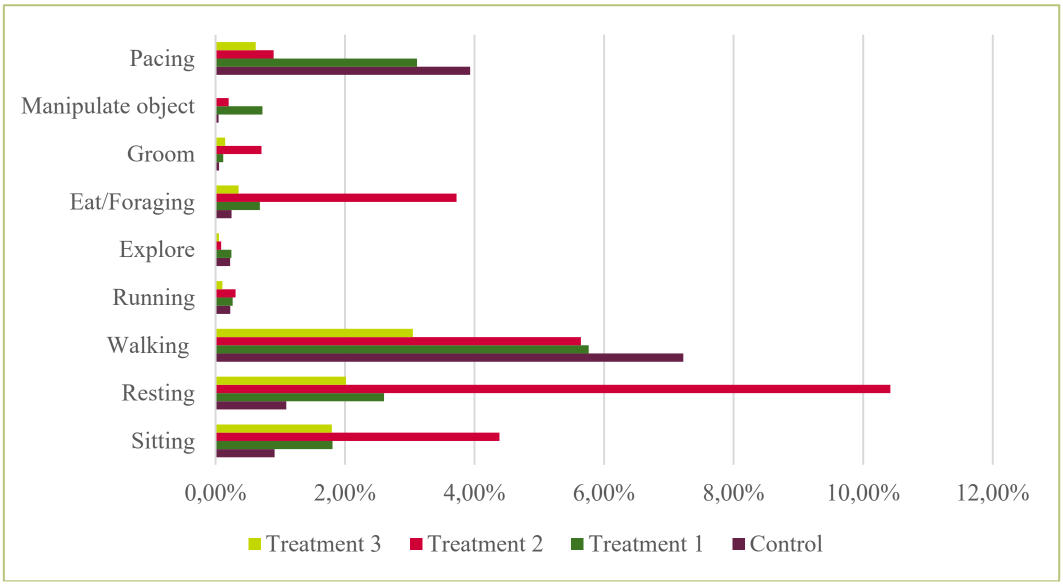


Figure 4. Percentage of time during the control and each treatment period in which behaviours exceeding 0.1% in at least one observation period were performed. 'Not visible' is not included.

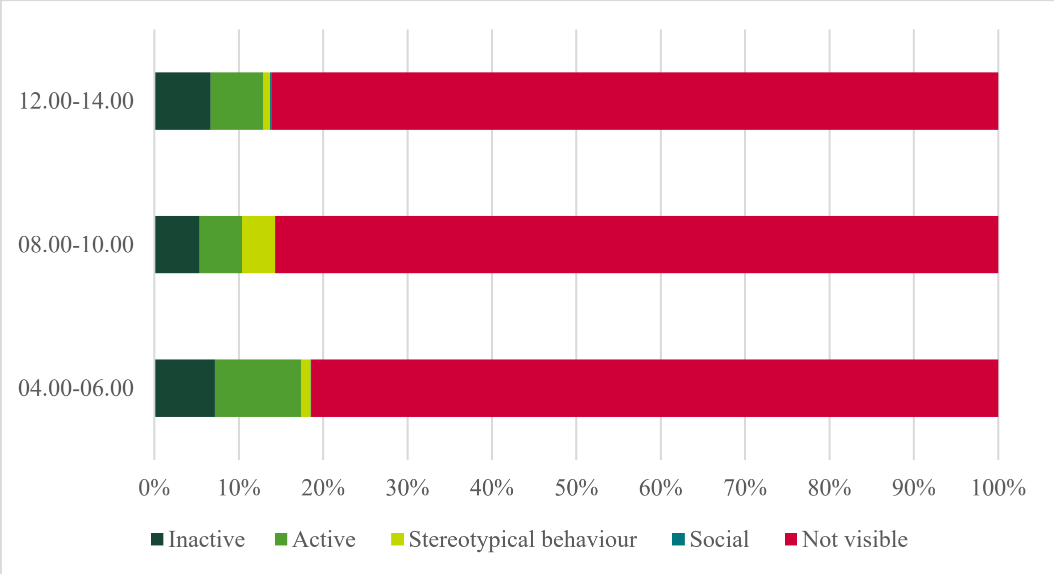


Figure 5. The percentage of time for each behaviour category in the ethogram (Tab. 1) for all observation periods over the whole study.

4.3 Pacing

Over the whole study period pacing decreased, with the largest mean during the control period and the lowest during treatment 3 (Fig. 6; Fig. 7). In treatment 1 the highest proportion of 'pacing' was observed but at the end of the treatment there was a large decrease in the behaviour (Fig. 7). For the majority of observations during treatment 2 and 3 no 'pacing' was seen (Fig. 7).

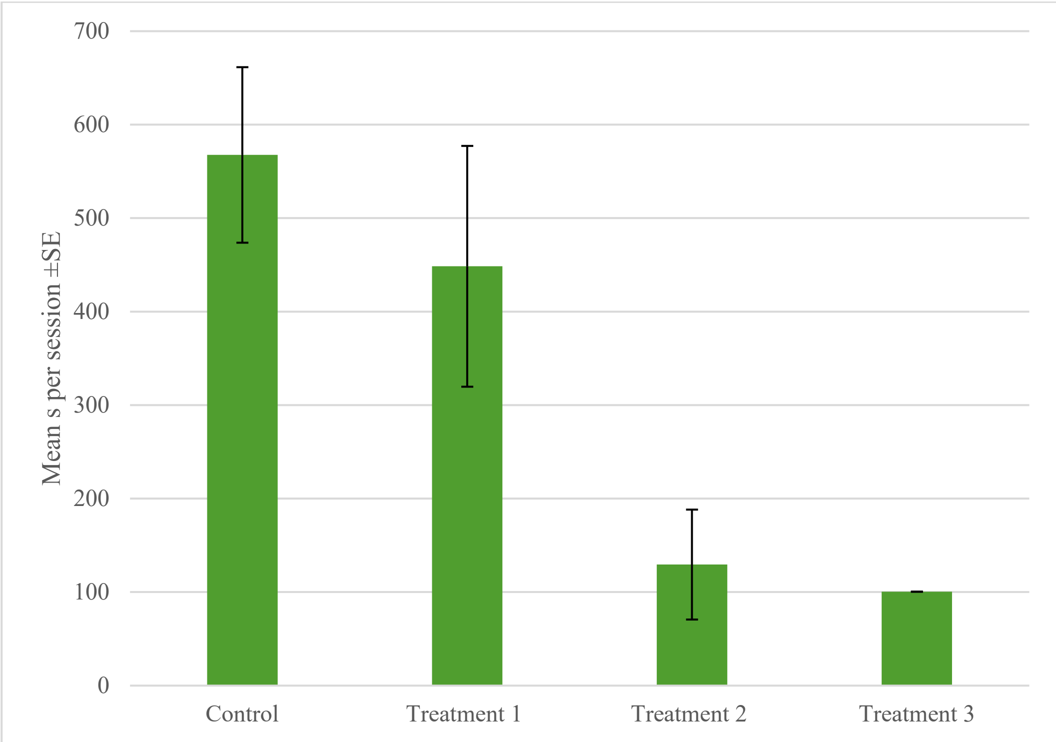
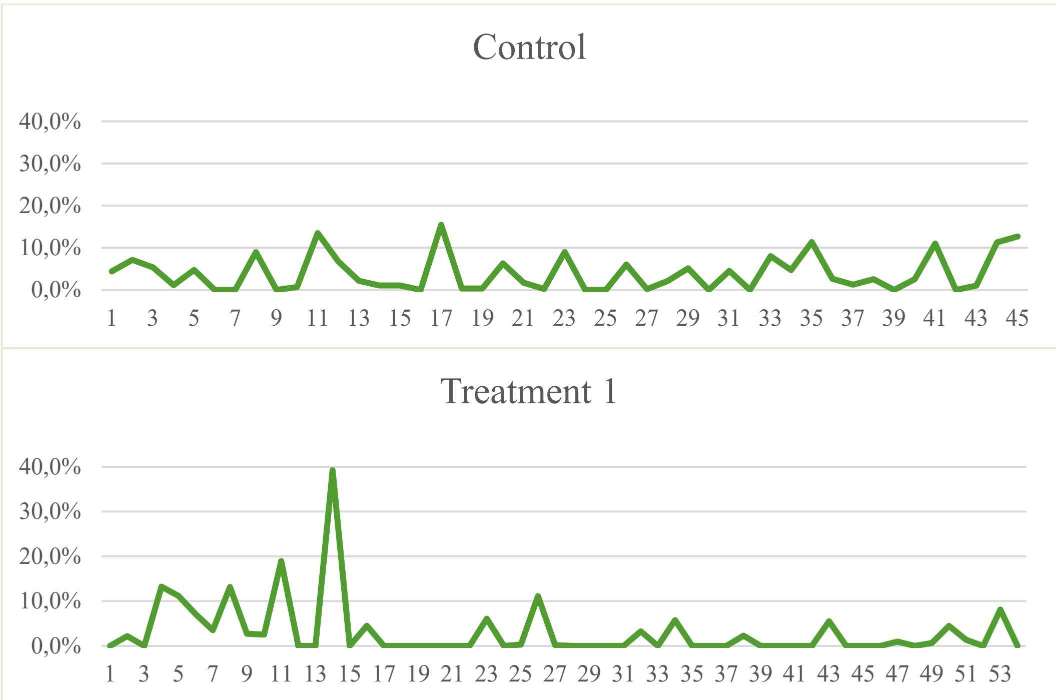


Figure 6. Descriptive statistics, mean and standard error of mean, in seconds for the behaviour 'pacing' during control and each treatment.



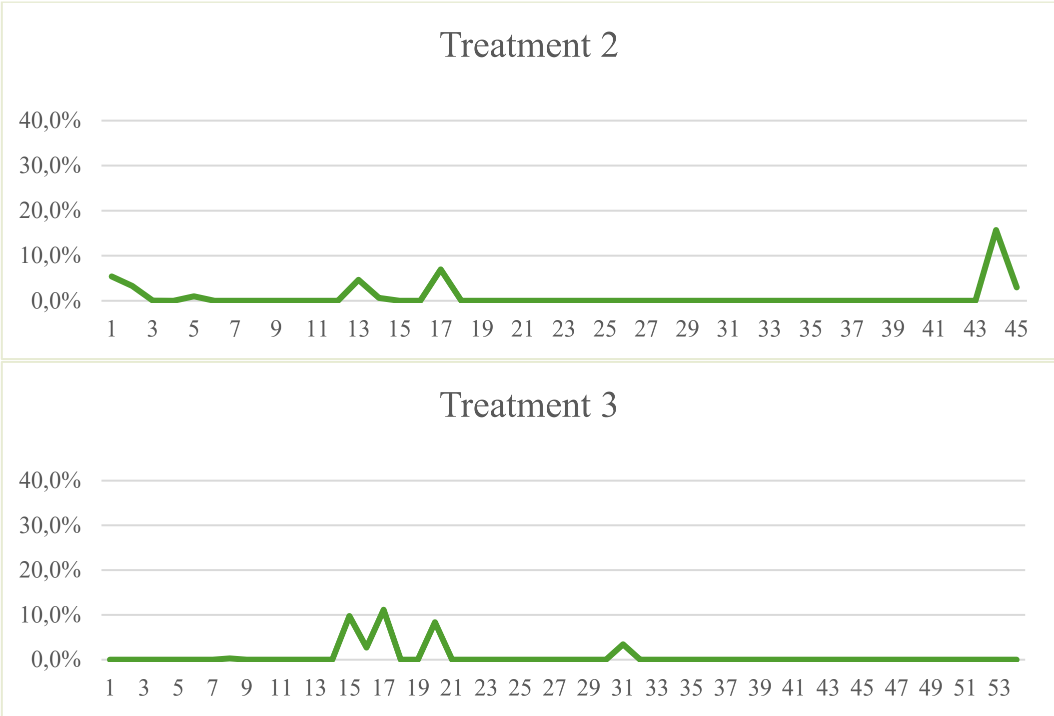


Figure 7. Percentage of pacing over time in each period of observation. The x-axis represents the observation session.

4.4 Activity in proximity

The negative binomial regression model identified multiple activities that were significantly associated with pacing behaviours (Tab. 3). The presence of keepers around the enclosure, cars and tractors were all associated with increased rates of pacing. Activities such as golf carts, horses and quadbikes passing by and bison activity was recorded but at such low frequency that they were removed from the statistical analysis. Bears waking up was also removed from the analysis due to the low frequency which created low certainty in the statistical analysis.

Table 3. *Results of the negative binomial regression analysis of factors affecting the frequency of pacing. Regression coefficients (β), incidence rate ratios (IRR = exp(β)), and p-values are shown for all predictors.*

Variable	**Estimate (β)**	**SE**	**IRR = exp(β)**	**p-value**
Keeper outside	-1.323	0.228	0.266	<0.001
Car	-1.121	0.363	0.326	0.002
Tractor	-1.101	0.386	0.333	0.004
Visitors	-0.533	0.495	0.587	0.282
Keepers inside	-1.669	0.699	0.188	0.017
Locked away	0.725	0.585	2.065	0.215

5. Discussion

5.1 Behavioural diversity

Over the observation period the behavioural diversity increased while at the same time pacing decreased (Fig. 2; Fig. 3). This can indicate an improvement in the lynxes' welfare since high behavioural diversity is often associated with fulfilled behavioural needs (Miller et al. 2020). A more diverse behavioural repertoire can also be an indication of lower stress levels. A study on cheetahs (*Acinonyx jubatus*) showed a positive correlation between high behavioural diversity and low faecal glucocorticoid metabolite levels (Miller et al. 2016). When natural behaviours such as foraging are stimulated through enrichment behavioural diversity often increases which these results support (Fig. 2; Fig 4) (Miller et al. 2020). Low behavioural diversity can be due to behavioural restriction, that the possibility of performing natural behaviours is removed due to limitation in the environment (Miller et al. 2020). Therefore, providing enrichment that stimulates behavioural needs such as foraging, which in this case removes the behavioural restriction of hunting behaviours, can be the cause of increase in behavioural diversity thus improving welfare.

5.2 Behaviour repertoire

The large proportion of 'not visible' during the study can be due to many different reasons. Carnivores in captivity often retreat from open spaces and hide when visitors are in the park (Suárez et al. 2017). For most of the study period the park was closed, however during treatment 3 the park was open for a few days which can explain the high proportion of 'not visible' during that study period. Even if no association between visitors and stereotypic behaviour was found in this study the large amount of 'not visible' can be an indication that the lynxes find visitors stressful. However, it can be argued that hiding during daylight may not indicate stress in lynxes, as they in the wild stay in coniferous forests by day and only move to open areas at nighttime (Fila et al. 2017). To investigate this further nighttime observations should be included in future studies since this was not possible in this study due to time constraints.

Another reason for the high proportion of 'not visible' is the time periods of the observations. The light conditions changed throughout the study, at the start the sunrise was at circa 08.30 while at the end the sunrise was around 05.30. The time for activity peaks for the lynxes changed time throughout the study since their activity is based on the light conditions (Heurich et al. 2014; Fila et al. 2017). This can explain why 'not visible' was observed at such a large proportion of the study, especially in treatment 3 when two out of three observations were performed during day light hours which is when lynxes normally are inactive and in hiding. Therefore, the high proportion of 'not visible' does not have to be an indication of stress but instead a sign that the lynxes' natural circadian rhythm is not disturbed.

Inactive behaviour is part of the lynx's daily activity and due to them following a crepuscular circadian pattern these behaviours are usually performed in the middle of the day (Fila et al. 2017). If Carpathian lynx follow their natural circadian rhythm in captivity is not researched, but a study on captive Iberian lynx (*Lynx pardinus*) showed that their natural activity pattern was not affected by captive environment (Yerga et al. 2015). The same activity pattern was observed in this study where the lynxes often were more inactive or not visible during daylight hours (Fig. 5). In treatment 2 there is a rather large increase in inactive behaviours (Fig. 3). During this treatment both lynxes spent a lot of time close to the full-body-feed, especially the female. The change in activity budget compared to control and other treatments may be a result from camera and enrichment placement. The positioning of the whole-body feed in front of a camera could have increased visibility by capturing animals that would otherwise be classified as 'not visible'. However, the data may also reflect an improvement in animal welfare, where the enrichment could have reduced stress-induced hiding behaviour (Suárez et al. 2017), if the assumption is that the high proportion of 'not visible' in other observation periods is hiding due to stress and not just preference of resting sites.

The increase in inactive behaviour can also be a consequence of gorging days when the animal gets full followed by fasting days with low effort (Kleinlugtenbelt et al. 2023). This can be beneficial for captive carnivores' welfare (Kleinlugtenbelt et al. 2023).

There is no research investigating how housing lynxes together in captivity affects them, but a behavioural study on snow leopards (*Panthera uncia*) indicated that housing them solitarily induces more stress compared to housing them in potential breeding pairs (Macri & Patterson-Kane, 2010). Another study on sand cats (*Felis margarita*), which is also a solitary felid, showed that social behaviours in captivity are few except during mating season (Bennett & Mellen 1983). These findings are supported by Pastorino et al. (2021), who observed that pair housing benefits captive leopard (*Panthera pardus*) welfare when enclosures allow individuals to avoid each other. Therefore, the low proportion of social behaviours throughout the whole study can be seen as an indication of good compatibility between the lynxes, increasing their welfare. The small increase in social behaviour observed during treatment 2 and 3 may be due to the timing of these treatments coinciding with the animals mating season (Svenska Rovdjursföreningen n.d; Bennett & Mellen 1983). Further studies on social behaviour and compatibility in potential breeding pairs in lynxes would be beneficial for further discussion regarding their welfare, since this is not well researched.

All treatments resulted in more ‘eating/foraging’ compared to control. During the treatments the lynxes had access to feed for a longer time in total compared to regular routines. In Treatment 2 the keepers saw a decrease in interest in the small pieces of feed they provide when walking around the enclosure, which may indicate that they were satisfied with the amount of feed the whole-body carcass provided. A reduction in stereotypic behaviours has been seen in other carnivores when provided with ad libitum feed (Houbak & Møller 2000; Clubb & Vickery 2006). The feeding schedule provided in this study might also be beneficial for reducing pacing as it mimics natural feeding behaviours in several ways. It creates gorging days that involve physical activity, interspersed with fasting days requiring minimal cognitive or physical effort, which is considered beneficial for captive obligate carnivores as it reflects hunting behaviour in the wild (Kleinlugtenbelt et al. 2023).

5.3 Pacing

The enrichments provided to the lynxes in this study were successful in reducing pacing. The enrichments were designed based on the lynx’s natural foraging behaviour in the wild and on the assumption from earlier research that pacing originates from an inability to perform hunting behaviours; the observed decrease in pacing may support this.

Pacing was not removed completely from the female’s behavioural repertoire. Stereotypic behaviour sometimes manifests in animals and is difficult to remove, it can become a kind of ‘can’t stop, won’t stop’ behaviour (Mason & Latham 2004). Therefore, a reduction in pacing might be the best indicator that the welfare has improved. No prior knowledge regarding the female’s history of pacing in previous facilities was attainable and how long a stereotypic behaviour must be performed to become established is dependent on the individual (Mason & Latham 2004), thus making it difficult to determine what triggered the behaviour from start.

In Treatment 1, only a slight decrease in pacing was observed. This may indicate that the enrichment used was less stimulating than those implemented during Treatments 2 and 3; however, other explanations are possible. At the beginning of Treatment 1, pacing occurred at a high frequency, followed by a gradual decline over time. In Treatments 2 and 3, the frequency of pacing was already much lower at the start compared to Treatment 1, suggesting that the behaviour had already been reduced and the low frequency was conserved from the enrichment in Treatment 1.Changing the order of the treatments could indicate the effect of each treatment if the study would be repeated. For example, if starting with Treatment 3 and ending with Treatment 1 would provide the same results the effect of the treatments might be the same and as mentioned above they give a gradual decrease and then the later treatments conserve the behavioural pattern. If instead, new results would show it could indicate that one of the treatments are more effective in reducing pacing. However, repeating a study with enrichments on the same individuals would remove the novelty effect of each treatment which is often an important part of successful enrichment (Mellen & Shepherdson 2007), and could therefore give a different result.

The large peak observed at the beginning of Treatment 1 may have been caused by stress associated with novel objects in the enclosure, as well as frustration from not being able to access the food immediately, since the animals were accustomed to receiving it as soon as the keepers left the enclosure (Burgener et al. 2008; Cless & Lukas 2017; Crane et al. 2017; Fitskie et al. 2024). Over time, however, they appeared to become habituated to the process of waiting for the winch to lower the food removing the stress from it.

Pacing was most common during the observation time between 08.00-10.00 which is when the keepers usually walk around the enclosure on specific dates. An association between keepers outside the enclosure and the pacing was found which can be due to anticipation or stress (Burgener et al. 2008; Cless & Lukas 2017; Fitskie et al. 2024).

5.4 Activity in proximity

Several variables were identified as significant predictors of pacing behaviour (Tab. 3), however the relatively small dataset limits the strength of the conclusions that can be drawn. In particular, variables that occurred rarely may have produced unstable parameter estimates, increasing uncertainty in the estimated effects. Despite these limitations, patterns emerged from the analysis. Pacing was positively associated with keepers walking around the enclosure and cars passing by or stopping near the enclosure which might be explained by anticipatory behaviour, especially keeper's activity (Burgener et al. 2008; Cless & Lukas 2017; Fitskie et al. 2024). The association between car and tractor activity with pacing may be stress-related, as lynxes in the wild have been observed to avoid areas close to human infrastructure (Fila et al. 2017).

There was no significant association between being locked away and keepers outside and pacing. However, in Treatment 2 there is a peak of pacing at the end of the treatment (Fig. 6) which was when both those environmental activities occurred which can indicate that it is a possible trigger for pacing. To conclude if being locked away has a significant impact on pacing, further studies are necessary since the frequency was low in this study.

During the statistical analysis no association between visitors and pacing was found however there was a low occurrence of visitors during the observations and further research is necessary for a conclusion to be drawn. The park was open during some days of Treatment 3 and on these days pacing increased (Fig. 6), which could reflect the visitors effect, since it has been seen in other lynxes and large felids (Suárez et al. 2017). During Treatment 3, no comparative analysis was performed to assess the effects of the enrichments during visitor hours versus periods when the park was closed. The small amount of available data was considered inadequate for producing reliable and meaningful results. To get a more certain result the study design would have to be more adapted to the zoo's opening hours. Even though the male never was observed performing pacing, the visitor effect may have influenced his welfare. The male might instead cope with the stress from visitors and other activities in proximity through hiding as seen in many large carnivores (Suárez et al. 2017).

The bears in the neighbouring enclosure woke up one time during the whole study, other than that specific activity, the bears' activity was unknown due to no observation of them. No statistical test could be performed due to limited amount of data. Therefore, it is not possible to determine whether the bears had an impact on the lynxes' welfare. In the wild, brown bears have an influence on lynx behaviour when it comes to movement patterns and hunting (Krofel & Jerina 2016), therefore it should not be rejected that they have an effect. In captive environments the possibility to avoid proximity to other predators is hindered which may cause stress. A study performed in a captive environment found that visual exposure to larger predators increased stress in Clouded leopards (*Neofelis nebulosa*) (Shepherdson et al. 2004).

The statistical analysis for activity in proximity would benefit from a longer study period to increase the frequency of all activities to get a more reliable result.

5.5 Treatment design

The reason for pacing in carnivores is often described as the restriction of hunting behaviour (Clubb & Vickery 2006). Zoo feeding regimes rarely mimic natural feeding behaviour in large carnivores (Kleinglugtenbelt et al. 2023). Therefore, when designing the treatments in this study creating enrichments that in some way reflected part of the hunting process in the wild was essential. Enrichment that allows expression of species-adapted hunting and ranging behaviours have been proven to improve captive carnivores' welfare (Clubb & Mason 2007).

Treatment 1

The winch and its settings during Treatment 1 was intended to remove the keepers' part of feeding. Before the study the lynxes could anticipate when they would be fed due the keepers always being near or inside parts of the enclosure to serve the food and shortly after that they were fed. With the winch the keepers still had to go inside the enclosure, but the feed was not available to the lynxes shortly after. Instead, they had to be alert for when the winch was lowered. This removed the anticipation that keepers often indicate feeding. Pacing has been observed in many carnivores due to anticipation from feeding (Burgener et al. 2008; Cless & Lukas 2017; Fitskie et al. 2024). Treatment 1 was designed to try to reduce the anticipatory factor and stimulate the alertness that is necessary for lynxes when hunting in the wild. There was a concern if the enrichment design could induce pacing due to frustration since the feed would be visible, but not attainable. However, since unpredictable feeding has been seen to reduce pacing (Clubb & Mason 2007; Kistler et al. 2009; Kleinglugtenbelt et al. 2023), the risk was deemed as low.

Treatment 2

Treatment 2 was designed to mimic the events after a successful hunt. In zoos, it is very common to skin and carve up the carcass before providing them to the animals (Kleinlugtenbelt et al. 2023). This removes the manipulation of a carcass lynxes are forced to do in the wild. The motive for the design of this enrichment was to stimulate the manipulation part of foraging by giving a whole-body feed. As it is common to feed small whole-body carcasses in captivity it was decided to use carcasses of roedeer, the largest prey lynxes hunt in the wild (Filla et al. 2017; Kleinlugtenbelt et al. 2023; Svenska Rovdjursföreningen n.d.). Large carcass feeding has not previously been evaluated in captive lynx of any subspecies even though it is one of their most common preys (Dul'a et al. 2023).

Treatment 3

The winch and its settings during treatment 3 was designed to reflect unsuccessful hunting. Therefore, the winch went up again after a short interval. If the lynxes did not become alert to the winch lowering quick enough, they would miss the feeding opportunity. Unpredictable feeding has been shown to be beneficial for carnivores to reduce pacing and feeding enrichments that include failure of obtaining feed, reflecting unsuccessful hunting, may improve welfare for carnivores (Clubb & Mason 2007; Kistler et al. 2009; Kleinglugtenbelt et al. 2023). The result in this study supports these findings, since pacing was reduced in both Treatment 1 and 3 where some predictability was removed by removing the correlation between keepers and feeding.

5.6 Reflections on method

For behavioural analysis frequency, duration and percent of time spent performing behaviour have a value in ethological studies (Altmann 1974). Continuous sampling collects both duration and frequency data of all behaviours by the observed individuals recorded during a specific period (Lehner 1992). It is an optimal method for behavioural data collection that captures rare and brief behavioural patterns, compared to other methods such as interval sampling (Tacha et al. 1985). Using continuous sampling made it possible to compare proportion of time spent pacing without the risk of missing any time spent pacing. If interval sampling was used, there was a risk that pacing was performed between scans removing vital data from the analysis. Also, instantaneous sampling may be less suitable for recording behaviours that are defined by their persistence over time, such as pacing, as those behaviours cannot be reliably identified from observations made at a single point in time (Altman 1974). However, two individuals were observed at the same time by one observer which creates the risk that brief behaviours were still missed due to the human factor. The usage of ad libitum sampling for activity in proximity removed the risk of missing activity that was not expected before the observations were performed.

The only difficulty was that in the program that was used, NX Witness Client, frame drops sometimes occurred making it difficult to pinpoint seconds of certain behaviours during continuous sampling. Sometimes this led to data collection of a behaviour at the time to either be prolonged or started shortly after the behaviour occurred. Nevertheless, this did not occur often and has no effect on the results because of the low occurrence of frame drops.

5.7 Limitations of the study

Multiple enrichments were provided and evaluated during the study, however due to the structure of the study it is not possible to determine how much effect each treatment had on reducing pacing. The method does not indicate if each treatment is as effective as the analysis shows, it might be that the diversity of all the treatments together provide enrichment that reduces pacing. Novelty and diversity increase the positive effect that enrichment can provide (Newberry 1995; Hall et al. 2018). The time between presentation of a new enrichment was very short, with only seven days between. Longer periods of time between each treatment would have been beneficial for the analysis of each enrichment. An improvement would have been to provide an enrichment for three weeks and then observe how long the effect of each treatment lasts, but due to time restrictions this was not possible. However, increasing the time between treatments would also increase variation in factors such as weather, visitor presence, and the timing of dusk and dawn, making it more difficult to determine what influenced the lynxes' behaviour.

Only two individuals were observed in the study and during data analysis the behavioural data was combined to represent the behavioural activity on group level. This was done to remove the risk of recording behaviour on the wrong individual. The individuals had different markings in the fur making it possible to differentiate them during daylight, however during dark hours the camera highlighted their light fur and thus removed visibility of their individual markings. A camera with better resolution when recording in the dark could help improve the study by improving visibility to distinguish between individuals.

In research performed in zoos, sample sizes are often much smaller compared to other areas of animal research (Holmes et al. 2020). Sometimes, in an effort to increase sample size, collaboration between different facilities keeping the same species are established (Kuhar 2006). Due to the time constraint of this project, collaboration with other facilities was not a possible solution to increase the low sample size. Increasing the sample size could have increased statistical power and reduce uncertainty in the result (Fernandez et al. 2025). However, it could also increase confounding factors or variables since environment, routines and keepers differ between zoos.

Another limitation is the relatively small sample size available for analysis of activity in proximity. While the negative binomial regression identified several significant associations with pacing behaviour, some explanatory variables were represented by few observations, which may have reduced the precision of the parameter estimates. This issue is reflected in the unstable coefficients observed for some variables. Therefore, the findings should be considered preliminary and would benefit from validation using a larger dataset.

It should also be noted that both age and sex may influence behavioural patterns and responses to enrichment. However, because this study included only two individuals, the potential effects of age and sex were not investigated further.

The observations were only performed during dusk and daylight, with no observation during dawn. However, this would have been interesting and could have provided a clearer understanding of how different types of enrichment impacts lynx behaviour since they are active in the wild during dawn (Fila et al. 2017). If longer time for the whole study period had been possible, including observation sessions at dawn and nighttime would have given a better portrayal of the daily activity pattern and further knowledge regarding effect of treatments.The cameras were positioned on the fence furthest from the road in the zoo and due to the coniferous forest in the enclosure the view to record activity in proximity was hindered. This might have had an impact on the data collection for this type of activity. There is a possibility that occurrences were undetected due to low visibility. An improvement would have been cameras positioned towards the road on the front fence of the enclosure.

In Treatment 3 a storm affected the study site and the function of the winch, and enrichment was not provided on the 6th of April. This happened at the same time as the park was open to visitors which makes it difficult to determine if it was the lack of enrichment or the visitors that increased pacing during Treatment 3.

5.8 Social and sustainability aspects

Biodiversity is rapidly decreasing and many, both researchers and the general public are anxious about the future concerning the loss of many species (Ceballos et al. 2017; Ceballos et al. 2020). To counteract the decline in species, zoos have changed their agenda to focus on conservation, education and research compared to earlier when it was mostly entertainment (Miranda et al. 2023). A conservation action that many zoos focus on is *ex situ* work through breeding programs in captivity (Miranda et al. 2023). Breeding programs are important to preserve or increase animal populations (Mallinson 1995). To have a successful breeding program good animal welfare is an important factor, otherwise animals in captivity might refrain from mating behaviour (Carlstead & Shepherdson 1994; Stier et al. 2012). Conserving the animals' natural behaviours is also an important part, the ability to perform natural behaviours have shown a decrease in stress and can help in the future during possible rewilding (Miller et al. 2016; Berg 2018; Chudeau et al. 2019). Stereotypic behaviours such as pacing can affect animals' behavioural diversity, it replaces natural behaviours and disrupts their activity pattern (Mason et al. 2007; Chudeau et al. 2019). Therefore, providing a good welfare for animals in captivity are important for conservation of biodiversity. The result in this study is helpful in this aspect by presenting enrichment that reduces stereotypic behaviour and increases the performance of natural behaviours.

A strong public interest in conservation is important to achieve a change and help biodiversity (deOliveria et al. 2023). Gaining public interest can be difficult, but studies have shown that if people can view animals in zoos their interest and support for conservation work increases (Fukano et al. 2020; Gregg et al. 2025). Zoo visitors are more receptive to information about conservation initiatives and are more likely to get involved in conservation work after their visit, even if they were previously opposed to it (Godinez & Fernandez 2019). However, a positive experience is essential to gain, and maintain, this interest (Miller 2011). Visitors' perception of a zoo and their interest in *ex situ* conservation work decreases when seeing stereotypic behaviour such as pacing (Miller 2011). Providing well adapted enrichment to animals to prevent and decrease pacing is not only important for the welfare of those individuals but is also an essential a part of successful conservation work.

5.9 Ethical aspects

Keeping wild animals in captivity is widely debated in conservation science and animal ethics and is often discussed in terms of the potential conflict between conservation goals and concerns about individual animal welfare (Minteer & Collins 2013). In conservation work there is often more focus on saving the population and not on the individual, which is central in an animal rights perspective (Minteer & Collins 2013). A moral concern in the discussion is which trade-offs are acceptable for protecting a species compared to an individual. Captive environments expose animals to challenges they are not faced with in the wild and can become stressful, but enrichment can help reduce stress and conserve natural behaviours (Solberg et al. 1999; Morgan & Tromborg 2007). Therefore, housing wild animals in captivity can be argued to be ethically justified if the environment provides enough stimulation of behavioural needs.

Pacing in the female lynx at Borås Zoo was a known welfare issue before the study was performed but enrichments were withheld to be able to have a control period. Withholding enrichment that may prevent abnormal behaviour could be considered ethically questionable from an animal welfare perspective. However, without a control period, it is not possible to determine whether the enrichment improves lynx welfare.

Ethical considerations in animal research are often discussed in relation to the 3Rs principles (Sherwin et al. 2003). The 3R's approach are based on the concepts of replacement, reduction and refinement and were first introduced by Russel & Burch in 1959 (Tannenbaum & Bennett 2015). The principles aim at reducing and eliminating distress for the individual (Tannenbaum & Bennett 2015).

Replacement means that, if possible, replace sentient beings with insentient material. Reduction means reducing the number of animals used in the study without decreasing the study's reliability. Lastly, refinement aims to decrease the occurrence or severity of inhumane procedures. The 3Rs principles are relevant to discuss in this study because it involved the use of captive animals and evaluated husbandry practices intended to improve animal welfare.

Replacement of animals is not applicable for this study since the aim is to evaluate how enrichment effects behaviour which requires direct observation of live animals. The lack of research on the effect of enrichment on stereotypic behaviour in Carpathian lynx also ethically justifies the usage of live animals since no comparison to earlier research is possible.

Reduction is not applicable for this study, only two animals were used since that was the number of individuals available. However, due to the small sample size the statistical reliability is limited. An increase in individuals could also be justified, not only by a stronger reliability in the result, but also that the study does not induce stress and instead their environment is enriched by the method.

Refinement is applied in the study design; the feeding enrichment may improve welfare and reduce stress. Nonetheless, a refinement of the study could have been increased continuous monitoring at the beginning of each treatment to ensure that the enrichment did not negatively impact the animals.

6. Conclusion

Feeding enrichment designed to stimulate the Carpathian lynx natural foraging behaviour has a positive impact on their behaviour by increasing behavioural diversity and reducing pacing behaviour. All treatments affected behaviour, however what effect each treatment had needs further evaluation with more time between each treatment. The provided enrichment types in this study can help improve welfare for lynx in captivity by removing behavioural restrictions in their environment.

Activity in proximity to the enclosure seems to trigger pacing, specifically keepers’ activity and vehicles, which might be anticipatory behaviour or stress related. However, due to the small sample size in this study, further research is needed to increase the reliability of the findings.

7. Thank you

Thank you to Lisa Lundin for being a great supervisor, by being very helpful and fast to answer my e-mails. Thank you to Borås Zoo for allowing me to work with your Carpathian Lynxes, it has been so much fun! Thank you to my friends who have helped and supported me through technical issues and everything writing a master thesis throws at you!

References

Allen, M., Rovero, F., Oberosler, V., Augugliaro, C., & Krofel, M. (2023). Effects of snow leopards (Panthera uncia) on olfactory communication of Pallas's cats (Otocolobus manul) in the Altai Mountains, Mongolia. Behaviour. 160(8-9). 807-815.

Altmann. J. (1974). Observational Study of Behavior: Sampling Methods. *Behaviour*. 49, 227-267.

Bashaw. M.J., Kelling. A.S., Bloomsmith. M.A., Maple. T.L. (2007). Environmental Effect on the Behavior of Zoo-housed Lions and Tiger, with a Case study on the Effects of a Visual Barrier on Pacing. Journal of Applied Animal Welfare Science. 10(2). 95-109.

Bennett. S.W., Mellen. J.D. (1983). Social Interactions and Solitary Behaviors in a Pair of Captive Sand Cats (*Felis margarita*). *Zoo Biology*. 2. 39-46.

Borås Djurpark (n.d.). Karpatiskt lodjur. https://www.borasdjurpark.se/djur/lodjur/ [2026-04-22]

Breitenmoser, U., Breitenmoser-Würsten, C., Lanz, T., von Arx, M., Antonevich, A., Bao, W. & Avgan, B. (2015). Lynx lynx (errata version published in 2017). The IUCN Red List of Threatened Species 2015: e.T12519A121707666. Accessed on 17 December 2025.

Burgener.N., Gusset. M., Schim. H. (2008). Frustrated Appetitive Foraging Behavior, Stereotypic Pacing, and Fecal Glucocorticoid Levels in Snow Leopards (Uncia uncia) in the Zurich Zoo. Journal of Applied Animal Welfare Science. 11(1). 74-83.

Cambrelen. D., Slater. M.N. (2023). Case study: Modifying repetitive behavior in a polar bear (Ursus maritimus). Zoo Biology. 42(3). 390-396.

Carlstead. K., Shepherdson. D. (1994). Effects of Environmental Enrichment on Reproduction. *Zoo Biology*. 13. 447-458.

Ceballos. G., Ehrlich. P.R., Dirzo. R. (2017). Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Ecology*. 114(30). E6089-E6096.

Ceballos. G., Ehrlich. P.R., Raven. P. H. (2020). Vertebrates on the brink as indicators of biological annihilation and the sixth mass extinction. *Environmental Sciences*. 117(24). 13596-13602.

Chudeau. K.R., Johnson. S.P., Caine. N.G. (2019). Enrichment reduces stereotypical behaviors and improves foraging development in rehabilitating Eastern Pacific Harbor Seals (*Phoca vitulina richardii*). 219. 104830.

Cless. I.T., Lukas. K.E. (2017). Variables affecting the manifestation of and intensiuty of pacing behaviour: A preliminary case study in zoo-housed polar bears. *Zoo Biology*. 36(5). 307-315.

Clubb. R., Mason. G.J. (2007). Natural behavioural biology as a risk factor in carnivore welfare: How analysing species differences could help zoos improve enclosures. Apllied Animal Behvaiour Science. 102(3-4). 303-328.

Clubb. R., Vickery. S. (2006). Locomotory Stereotypies in Carnivores: Does Pacing Stem from Hunting, Ranging or Frustrated Escape? In: Mason. G., Rushen. J. Stereotypic Animal Behaviour Fundamentals and Applications to Welfare. 2nd edition. CABI. 58-85.

Cornhill. K.L., Kerley. G.I.H. (2020). Cheetah communication at scent-marking sites can be inhibited or delayed by predators. Behavioral Ecology and Sociobiology. 74, 21.

Crane. A. L., Ferrari. M.C.O. (2017). Patterns of predator neophobia: a meta-analyctic review. *Proc Biol Sci* 281(1861). 20170583

Damasceno. J., Genaro. G., Quirke. T., McCarthy. S., McKeown. S., O´Riordan. R. (2017). The effects of intrinsic enrichment on captive felids. Zoo Biology. 36, 186-192.

Davey. G. (2007). Visitors' Effects on the Welfare of Animals in the Zoo: A Review. Journal of Applied Animal Welfare Science. 10(2), 169-183.

deOliveira Caetano, G. H., Vardi, R., Jarić, I., Correia, R. A., Roll, U., & Veríssimo, D. (2023). Evaluating global interest in biodiversity and conservation. *Conservation Biology*. 37. e14100.

Dul'a. M., Nicol. C., Bojda. M., Labuda. J., Slamka. M., Kutal. M. (2023). The first insight into hunting and feeding behaviour if the Eurasian Lynx in the Western Carpathians. *Mammal Research*. 68. 237-242.

European Association of Zoos and Aquaria. (2025). EAZA Ex-situ Programme Overview August 2025. European Association of Zoos and Aquaria.

Fernandez. E.J., Brereton. J.E., Tuke. J. (2025). Learing your indiviudal infrences. A guide for overcoming statistical challenges in small- N studies. *Applied Animal Behaviour Science*. 292. 106804.

Filla. M., Premier. J., Magg. N., Dupke. C., Khorozyan. I., Waltert. M., Bufka. L., Heurich. M. (2017). Habitat selection by Eurasian lynx (Lynx lynx) is primarily driven by avoidance of human activity during day and prey availability during night. Ecology and Evolution. 7, 6367-6381.

Fitskie. L., Kappelhof. J., Cunha. F. (2024). Effects of Rando, Feeding Schedule on Pacing in Asiatic Lions (*Panthera leo persicus*). *Zoo Biology.* 43(6). 590-594.

Fukano. Y. Tanaka. Y., Soga. M. (2020). Zoos and animated animals increase public interest in and support for threatened animals. *Science of The Total Environment*. 704. 135352.

Godinez. A.M., Fernandez. E.J. (2019). What IS the Zoo Experience? How Zoos Impact a Visitor's Behaviors, Perceptions, and Conservation Efforts. *Front Psychol.* 10. 1746.

Gosling. L.M., Roberts. S.C. (2001). Scent -marking by male mammals: Cheat-proof signals to competitors and mates. Advances in the Study of Behavior, 30. 169-217.

Gregg. E.A., Garrard. G.E., Bekessy. S.A., Kusmanoff. A. M., Martin. J.K., Sleinske. M.J., Kidd. L.R., Robinson. J.A. (2025). Barriers to public engagement with biodiversity conservation. *Conservation Biology*. 39(4). E70078.

Hall. B.A., Melfi. V., Burns. A., McGill. D.M., Doyle. R.E. (2018). Curious creatures: a multi-taxa investigation of responses to novelty in a zoo environment. *PeerJ*. 6. e4454.

Heurich. M., Hilger. A., Küchenhoff. H., Andrén. H., Bufka. L., Krofel. M., Mattisson. J., Odden. J., Persson. J., Rauset. G.R., Schmidt. K., Linnell. J.D. (2014). Activity Patterns of Eurasian Lynx Are Modulated by Light Regime and Individual Traits over a Wide Latitudinal Range. PLoS ONE. 9(12). E114143.

Hofstra. W.A., de Weerd. A. W. (2008). How to assess circadian rhythm in humans: A review of literature. Epilepsy & Behavior. 13(3), 438-444.

Holmes. L., Edwards. K., Moss. A. Tollington. S., Fowler. A., Hughes. D., Sudell. M. (2020). Statistics at the zoo. *Significance*. 17(5). 26-29.

Hosey. G.R. (2000) Zoo Animals and Their Human Audiences: What is the Visitor Effect? Animal Welfare. 9(4), 343-357.

Kistler. C., Hegglin. D., Würbel. H., König. B. (2009). Feeding ernichment in an opportinistic carnivore: The red fox. *Applied Animal Behaviour Science*. 116(2-4). 260-265.

Kleinlugtenbelt. C., Clauss. M., Burkevica. A., De Cuyper. A. (2023). Fasted and furious? Considerations on the use of fasting days in alrge carnivore husbandry. *Journal of Zoo and Aquarium Research.* 11(3). 318-323.

Kleinlugtenbelt. C.L.M., Burkevica. A., Clauss. M. (2023). Large carnivore feeding in European zoos. *The Zoological Garden*. 91. 9-39.

Krofel. M., Jerina. K. (2016). Mind the cat: Conservation management of a protected dominant scavenger indirectly affects an endangered apex predator. *Biological Conservation*. 197. 40-46.

Kuhar. C.W. (2006). In the Deep End: Pooling Data and Other Statistical Challenges of Zoo and Aquarium Research. *Zoo Biology*. 25. 339-352.

Lehner. P.N. (1992). Sampling Methods in Behavior Research. *Poultry Science*. 71, 643-649.

Liang, Y., Kramer-Schadt, S., Mattisson, J., Belotti, E., Bufka, L., Melovski, D., Slana, D., Anders, O., Middelhoff, T.L., Andren, H., Aronsson, M., Persson, J., Skorupski, J., Tracz, M., Tracz, M., Grzegorzek, M., Baryło, R., Bauduin, S., Vandel, J.M., Ĝ Erne, R., Trajbarič, A., Duľa, M., Kutal, M., Flež Ar, U., Hočevar, L., Krofel, M., Oliveira, T., Gomerčić, T., Topličanec, I., Kubala, J., Tám, B., Krojerová-Prokešová, J., Kont, R., Kowalczyk, R., Schmidt, K., Linnell, J.D.C., Odden, J., Molinari-Jobin, A., Mysłajek, R.W., Nowak, S., Figura, M., Okarma, H. & Ornicā Ns, A. (2026). Extra-territorial excursions of Eurasian lynx (Lynx lynx) during the mating season across Europe. Proceedings of the Royal Society B : Biological Sciences, 293 (2063).

Lyons. J., Young. R.J., Deag. J.M. (1997). The Effects of Physical Characteristics of the Environment and Feeding Regime on the Behavior of Captive Felids. Zoo Biology. 16, 71-83.

Macri. A.M., Patterson-Kane. E. (2010). Behavioural analysis of solitary versus socially housed snow leopards (*Panthera uncia*), with the provision of simulated social contact. *Applied Animal Behvaiour Science*. 130(3-4), 115-123.

Mallinson. J.J.C. (1995). Conservation breeding programmes: an important ingredient for species survival. *Biodiversity and Conservation*. 4. 617-635.

Marinath. L., Vaz. J., Kumar. D., Thiyagesan. K., Baskaran. N, (2019). Drivers of stereotypic behaviour and physiological stress among captive jungle cat (Felis chaus Schreber, 1777) in India. Physiology & Behavior. 210, 112651.

Mason. G., Clubb. R., Latham. N., Vickery. S. (2001). Why and how should we use environmental enrichment to tackle stereotypic behaviour? Applied Animal Behaviour Science. 102(3-4). 163-188). https://www.sciencedirect.com/science/article/pii/S0168159106001900

Mason. G., Clubb. R., Latham. N., Vickery. S. (2007). Why and how should we use environmental enrichment to tackle stereotypic behaviour? Applied Animal Behaviour Science. 102, 163-188.

Mason. G., Latham. N. (2004). Can't stop, won't stop: is stereotypy a reliable animal welfare indicator? *Animal Welfare*. 13(S1). 57-69.

Mellen. J.D., Shepherdson. D.J. (2007). Environmental enrichment for felids: an integrated approach. *International Zoo Yearbook*. 35(1), 191-197.

Miller. L.J. (2011). Visitor reaction to pacing behavior: influence on the perception of animal care and interest in supporting zoological institutions. *Zoo Biology*. 31(2). 242-248.

Miller. L.J., Pisacane. C.B., Vicino. G.A. (2016). Relationship between behavioural diversity and faecal glucocorticoid metabolites: a case study with cheetahs (*Acinonyx jubatus*). *Animal Welfare.* 25. 325-329.

Miller. L.J., Vicino. G.A., Sheftel. J., Lauderdale. L.K. (2020). Behavioural Diversity as a Potential Indicator of Positive Animal Welfare. Animals. 10(7). 1211.

Minteer. B.A., Collins. J.P. (2013). Ecological Ethica in Captivity: Balancing Values and Responsibilities in Zoo and Aquarium Research under Rapid Global Change. *ILAR Journal.* 54. (1). 41-51.

Miranda. R., Escribano. N., Casas. M., Pino-del-Carpio. A., Villaroya. A. (2023). The role of Zoos and Aquariums in a Changing World. *Annual review Animal Biosciences*. 11.287-306.

Morgan. K.N., Tromborg. C.T. (2007). Sources of stress in captivity. Applied Animal Behaviour Science. 102, 3-4.

Newberry. R.C. (1995). Environmental enrichment: Increasing the biological relevance of captive environments. *Applied Animal Behaviour Science.* 44(2-4). 229-243.

Nordens Ark (n.d.). Lodjur. https://nordensark.se/djuren/daggdjur/lodjur/ [2026-04-22]

Pastorino. G.Q., Brereton. J.E., Drago. F., Mazzonetto. F., Confalonieri. E., Preziosi. R. (2021). Investigating the effect if social grouping on the behaviours of captive leopards. *Jouranl of Zoo and Aquarium Research.* 9(6). 116-123.

Rabin. L.A. (2003). Maintaining Behavioural Diversity in Captivity for Conservation: Natural Behaviour Management. *Animal Welfare*. 12(1). 85-94.

SFS 2018:1192. Animal Welfare Act.

SFS 2019:66. Animal Welfare Ordinance.

Shepherdson. D.J., Carlstead. K.C., Wielebnowski. N. (2004). Cross-institutional assessment of stress responses in zoo animals using longitudinal monitoring of faecal corticoids and behaviour. *Animal Welfare*. 13. 105-113.

Sherwin. C.M., Christiansen. S.B., Duncan. I.J., Erhard. H.W., Lay Jr. D.C., Mench. J.A., O'Connor. C.E., Petherick. J.C. (2003). Guidelines for the ethical use of animals in applied ethology studies. *Applied Animal Behaviour Science*. 81(3). 291-305.

SJVFS 2019:29. Swedish Board of Agriculture's regulations and general advice on animal keeping in zoos.

Skibiel. A.L., Trevino. H.S., Naugher. K. (2007). Comparison of Several Types of Enrichment for Captive Felids. Zoo Biology. 26, 371-381.

Solberg. L.C., Horton. T.H., Turek. F.W. (1999). Circadian rhythms and depression: effects of exercise in an animal model. American Journal of Physiology-Regulatory, Integrative and Comparative Physiology. 276(1), 152-161.

Spiezio. C., Galardi. E.G., Sandri. C., Regaiolli. B. (2023). Do not disturb: Visitors' effect on the behavior and welfare of female and male big cats in zoos. Zoo biology. 42(6), 744-756.

Stier. A., Reichert. S., Massemin. S., Bize. P., Criscuolo. F. (2012) Constraint and cost of oxidative stress on reproduction: correlative evidence in laboratory mice and review of the literature. *Frontiers of Zoology*. 9. 37.

Suárez. P., Recuerda. P., Arias-de-Reyna. L. (2017). Behaviour and welfare: the visitor effect in captive felids. Animal Welfare. 26(1), 25-34.

Svenska Rovdjursföreningen (n.d.). Lodjur. https://rovdjur.se/rovdjuren/lodjur/ [2026-04-22]

Swaisgood. R.R., Shepherdson. D.J. (2005). Scientific approaches to enrichment and stereotypies in zoo animals: what´s been done and where should we go next? Zoo Biology. 24, 499-518.

Tacha. T.C., Vohs. P.A., Iverson. G.C. (1985). A Comparison of Interval and Continuous Sampling Methods for Behavioural Observations. *Journal of Field Ornithology*. 56, 258-264.

Tannenbaum. J., Bennett. B.T. (2015). Russell and Burch's 3Rs Then and Now: The need for Clarity in Definition and Purpose. *J Am Assoc Lab Anim Sci.* 54(2). 120-132.

Tuite. E.K., Moss. S.A., Phillips. C.J., Ward. S.J. (2022). Why Are Enrichment Practices in Zoos Difficult to Implement Effectively? Animals. 12(5), 554.

Vogt. K., Zimmermann. F., Kölliker. M., Breitenmoser. U. (2014). Scent-marking behaviour and social dynamics in a wild population of Eurasian lynx Lynx lynx. Behavioural Processes. 106. 98-106.

Walker. W.H. Walton. J.C., DeVries. A.C., Nelson. R.J. (2020). Circadian rhythm disruption and mental health. Translational Physchiatry. 10, 28.

Watters. J.V., Krebs. B.L., Eschmann. C.L. (2021). Assessing Animal Welfare with Behavior: Onward with Caution. *J. Zool. Bot. Gard.* 2(1). 75-87.

Yerga. J., Calzada. J., Manteca. X., Vargas. A., Pérez. M.J., Palomares. F., Rivas. A. (2015). Ontogeny of daily activity and circadian rhythm in the Iberian lynx (*Lynx pardinus*).

Ödberg. F.O. (1987). The influence of cage size and environmental enrichment on the development of stereotypies in bank voles (Clethrionomys glareolus). Behavioural Processes. 14(2). 155-173.

Popular science summary

The Carpathian Lynx (*Lynx Lynx carpathicus*) is a subspecies to the Eurasian lynx (*Lynx Lynx*). The species is of least concern according to the IUCN Red List. Earlier, hunting and diseases have decreased the Eurasian lynx population size, but due to successful conservation work the population has expanded. As part of the conservation efforts of EAZA (European Association of Zoos and Aquaria) for the lynx, a breeding pair is housed at Borås Zoo. In the wild, the Carpathian lynx lives in dense forests during daytime and meadows during nighttime. Their activity is dependent on light conditions, and they are most active during twilight.

Wild animals kept in captivity can be exposed to a large amount of stress due to new challenges in the captive environment compared to challenges in the wild. This can cause stress and negatively impact their welfare. This can lead to stereotypic behaviours such as pacing, when the animals try to cope with the effects of captivity. Providing enrichment adapted to the species' natural behaviours can help with reducing stereotypic behaviours by stimulating their behavioural needs.

The female Carpathian Lynx at Borås zoo had developed pacing and performed it daily showing a need for improvement in the environment. The aim of this study was to explore possible triggers for her pacing and provide three different enrichments and evaluate if they helped in reducing pacing. The enrichments were decided with the lynxes natural hunting behaviour in mind.

The first part of the study was the control, during this, regular routines were followed and no new enrichments were given. After the control period, Treatment 1 was initiated. During this the lynxes were provided with feed using a winch that went down during dusk, when the lynx usually hunts. This enrichment was provided five times during Treatment 1. Thereafter, Treatment 2 was implemented which included full-body feeding of a roe deer carcass tied to a tree. Enrichment was provided three times during this treatment. The last part of the study was Treatment 3 which included the winch with feed again. However, it had different settings which made it lower and raise the feed multiple times during dusk and dawn on enrichment days. Enrichment was provided five times during Treatment 3. Activity around the enclosure was recorded for analysis of possible triggers for pacing during the whole study.

The results showed that enrichment designed after the lynx's natural foraging behaviour is effective for reducing stereotypic behaviours, specifically pacing. In Treatment 1 there was not a large reduction of pacing, however there was a gradual decrease throughout the treatment. During Treatment 2 and 3 pacing was successfully reduced to zero percentage of time on most the observation days. Due to the study design, it is difficult to determine how much effect each treatment individually had. For further evaluation more time between each treatment is necessary. However, it is possible to conclude that the provided enrichments help improve welfare for lynx in captivity by improving the environment. The results for activity near the enclosure showed that keepers' activity and vehicles might trigger pacing. The reason for this could be that they anticipate something when the keepers are close such as feeding or other enrichments. It could also be stress related.

However, this is a study with small sample size, so further research is needed to increase certainty in the result.

Publishing and archiving

Approved students' theses at SLU can be published online. As a student you own the copyright to your work and in such cases, you need to approve the publication. In connection with your approval of publication, SLU will process your personal data (name) to make the work searchable on the internet. You can revoke your consent at any time by contacting the library.

Even if you choose not to publish the work or if you revoke your approval, the thesis will be archived digitally according to archive legislation.

You will find links to SLU's publication agreement and SLU's processing of personal data and your rights on this page:

- https://libanswers.slu.se/en/faq/228318

☒ YES, I, Linnéa Boije, have read and agree to the agreement for publication and the personal data processing that takes place in connection with this

☐ NO, I/we do not give my/our permission to publish the full text of this work. However, the work will be uploaded for archiving and the metadata and summary will be visible and searchable.