Effects of food-based enrichment on enclosure use and behavioral patterns in captive mammalian predators: a case study from an Austrian wildlife park (#80198)

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Effects of food-based enrichment on enclosure use and behavioral patterns in captive mammalian predators: a case study from an Austrian wildlife park

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Background. Combining naturalistic enclosure design and animal welfare with visitor interests and education can be challenging for zoos and wildlife parks. To accomplish both purposes, different types of enrichment (non-food-based items, such as environmental, sensory, cognitive, social, or food-based items) can be used. The aim of the present study is to investigate the effect of food-based and olfactory enrichments on enclosure use, behavior, and visibility of captive brown bears (*Ursus arctos*), pine martens (*Martes* martes), domestic ferrets (Mustela putorius furo), and golden jackals (Canis aureus). **Methods.** We used observational approaches to measure enclosure use, behavior, and visibility during three different experimental phases: (1) pre-enrichment (baseline, no experience with the enrichment yet), (2) during enrichment (enrichment was provided at low frequented locations in the enclosures that are easily visible to visitors), and (3) postenrichment (enrichment was removed from the enclosures). In addition, visitors' perception of animal visibility and enclosure design was examined using a questionnaire. **Results.** We found that enrichment led to a uniform use of the enclosure and enhanced visibility in brown bears, increased activity budgets in pine martens, and high object interaction in both species. No effects of enrichment were observed in domestic ferrets. Golden jackals did not leave their burrows during daytime during the entire observation period; thus, observations were not possible at all. Furthermore, questionnaires from 86 participants showed that visitors experience enclosures very differently. The visitors generally reported enough resting places, appreciated the brown bear and golden jackal enclosures, and the majority rated the enclosures as natural. But, they also perceived a lack of enclosure space for the pine martens, domestic ferrets, and golden jackals, as well as a lack of stimulation for activity in general. Our results may indicate that food-based

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enrichment can affect enclosure use, temporal activity patterns, and animal visibility. However, these finding must be interpreted with caution as the results were inconsistent across species. This may suggest that food-based-enrichment may need to be selected on a species-specific basis in order to have a positive impact on the welfare of captive animals.



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3	predators: a case study from an Austrian wildlife park
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Abstract

Background. Combining naturalistic enclosure design and animal welfare with visitor interests and
education can be challenging for zoos and wildlife parks. To accomplish both purposes, different types of
enrichment (non-food-based items, such as environmental, sensory, cognitive, social, or food-based
items) can be used. The aim of the present study is to investigate the effect of food-based and olfactory
enrichments on enclosure use, behavior, and visibility of captive brown bears (Ursus arctos), pine
martens (Martes martes), domestic ferrets (Mustela putorius furo), and golden jackals (Canis aureus).
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enclosures that are easily visible to visitors), and (3) post-enrichment (enrichment was removed from the
enclosures). In addition, visitors' perception of animal visibility and enclosure design was examined using
a questionnaire.
Results. We found that enrichment led to a uniform use of the enclosure and enhanced visibility in
brown bears, increased activity budgets in pine martens, and high object interaction in both species. No
effects of enrichment were observed in domestic ferrets. Golden jackals did not leave their burrows
during daytime during the entire observation period; thus, observations were not possible at all.
Furthermore, questionnaires from 86 participants showed that visitors experience enclosures very
differently. The visitors generally reported enough resting places, appreciated the brown bear and golden
jackal enclosures, and the majority rated the enclosures as natural. But, they also perceived a lack of
enclosure space for the pine martens, domestic ferrets, and golden jackals, as well as a lack of stimulation
for activity in general. Our results may indicate that food-based enrichment can affect enclosure use,
temporal activity patterns, and animal visibility. However, these finding must be interpreted with caution
as the results were inconsistent across species. This may suggest that food-based-enrichment may need to
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59	Keywords: animal visibility, brown bear, domestic ferret, pine marten, visitor experience, animal
60	welfare, zoo experience
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Introduction

In captivity, enclosures often lack biological and ecological conditions that can be found in the
natural habitat of the animals. For instance, zoo-housed animals frequently have less space available than
they would use in the wild and lack enclosure complexity, which can create stress and stereotypic
behaviors (Rose et al. 2017; Mellor et al. 2018). Among other approaches, enrichment is most commonly
used to reduce and prevent the development of abnormal behaviors, to stimulate activity, and to enhance
high-quality of life for the animals (Mason et al. 2007). Enrichments are classified into non-food-based
items, such as environmental (e.g. water element, climbing structure), sensory (e.g. mirrors, scratch
poles), cognitive (e.g. novel object, puzzle feeder), or social (e.g. conspecifics, mixed species enclosures,
human-animal interactions) stimuli, and food-based items (Swaisgood and Shepherdson 2005).
Enrichment can stimulate animals' activities in previously underused enclosure areas, thereby
allowing an efficient use of the available space and promoting the uniform use of different zones (Renner
and Lussier 2002; Lawrence et al. 2021). For instance, Indian Leopards (Panthera pardus) showed a
higher use of environmentally enriched zones within their enclosure, and thereby increased the use of
certain areas, rather than using only a few of them (Mallapur et al. 2010). The extent to which the space
of an enclosure is used is considered an indicator for the animal's welfare, as a non-uniform use of the
enclosure could be related to inappropriate design (Ross et al. 2009). Naturalistic environments reflect the
respective home range size in the wild and offer hiding places for the animals, which is often
accompanied by low animal visibility for the visitors (Bitgood et al. 1988). By contrast, other studies
claim that enrichment increases the visibility of captive animals (Foerder et al. 2020). Both aspects, i.e.
high animal visibility and the possibility of observing a species' behaviors (e.g. social interactions,
locomotion, grooming) fosters and maintains visitor interest (Bitgood et al. 1988; Kirchgessner and
Sewall 2015) and thus can promote public education, enable research and conservation efforts (Fernandez
et al. 2009; Kuhar et al. 2010).
In order to stimulate natural species-typical behavioral patterns, both the type and the timing when
an enrichment is introduced are important (Kuczaj et al. 2002). In fact, zoo-housed animals often show





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very different behavioral patterns in comparison with individuals of the same species living in the wild (Schneider et al. 2014; Inoue and Shimada 2020). For instance, explorative behavior related to acquisition and consumption of food might be remarkably absent in zoos. Western lowland gorillas (Gorilla gorilla gorilla) in human care increased their activity budget reminiscent of individuals observed in the wild when feeding schedules varied, rather than providing food at fixed times (Charmoy et al. 2015). Similar findings were reported for cheetahs (Acinonyx jubatus), when feeding schedules, feeding locations, and olfactory enrichment varied (Quirke and Riordan 2011). Determining temporal behavior patterns and activity budgets in captivity is particularly relevant for species that would allocate most of their active time to food procurement in the wild. In addition, the diversity of the natural behavioral repertoire displayed by a species in captivity may increase when introducing enrichment to the enclosure (Swaisgood and Shepherdson 2005; McPhee and Carlstead 2010). Spectacled bears (Tremarctos ornatus) displayed more behaviors similar to their wild counterparts after introducing climbing structures and other environmental items (Renner and Lussier 2002). Furthermore, forms of food-based enrichment, including the use of novel objects to increase the difficulty and time to acquire food, can positively affect the behavioral repertoire of captive animals. Kodiak (*Ursus arctos middendorffi*), polar (*Ursus maritimus*), and Asiatic black bears (*Ursus thibetanus*) were provided with ice treats (i.e. ice blocks filled with food), which resulted in higher activity and reduced presence of abnormal behavior during enrichment sessions (Forthman et al. 1992). Furthermore, when European wolves (Canis lupus lupus) were exposed to food hidden in pouches or plastic food balls in the enclosure, stereotypic behaviors and negative social behaviors decreased, and they exhibited more exploratory behavior (Riggio et al. 2019). Lack of space or lack of enrichment may have detrimental effects on animal behavior, such as fewer social interactions (e.g. chimpanzees (*Pan troglodytes*), Koyama and Aureli 2019) or even the occurrence of stereotypic behaviors (e.g. carnivores, ungulates,

rodents, and primates, Mason et al. 2007; chickens (Gallus gallus), Dixon et al. 2010). Natural species-

specific behaviors are, however, necessary for fitness and consequently for zoos' conservation efforts for

endangered species. Furthermore, zoo visitors may perceive abnormal behaviors as the animal being





'unhappy' or 'unhealthy' (McPhee and Carlstead 2010), which could have a negative impact on the educational message of the zoo (Fernandez et al. 2009; Godinez and Fernandez 2019). Thus, displaying natural species-typical behaviors is not only crucial for animal welfare, but also for the zoo management in order to maintain visitors' interest and satisfaction (McPhee and Carlstead 2010).

Measuring zoo visitors' view on animal welfare and enclosure design is necessary in order to identify expectations of zoo visitors (Davey 2006; Lee 2015). When surveyed, zoo visitors rated naturalistic enclosure designs as favorable, because they perceived enhanced animal welfare (Price et al. 1994). Visibility and behavior of captive animals also influenced visitors' perception and attitude towards animal welfare (Salas et al. 2021). Negative perceptions of animal welfare were associated with the occurrence of stereotypic behaviors, while visitors' enjoyment was associated with animal visibility (Godinez et al. 2013). Furthermore, evaluating visitors' expectations fosters understanding how to keep exhibits interesting and enjoyable, but also to gain knowledge which aspects of environmental education and conservation should be promoted and improved (Davey 2006). Thus, recognizing the different expectations of zoo visitors regarding enclosure design and animal welfare can help to inform zoo management about necessary improvements (Tomas et al. 2003).

The aim of this study was to determine the effect of enrichment (food-based and sensory, i.e. olfactory, items) on enclosure use, behavior and visibility (i.e. number of individuals visible at a moment) of four carnivorous mammalian species in human care in a wildlife park setting: brown bears (*Ursus arctos*), pine martens (*Martes martes*), domestic ferrets (*Mustela putorius furo*), and golden jackals (*Canis aureus*). Several reasons supported the choice of these four species, which was taken in coordination with the Wildlife Park management: first, all four species showed little and non-uniform use of enclosure space; second, visibility of the individuals was low in two of the enclosures (i.e. golden jackals and ferrets; Cumberland Wildlife Park, personal communication); and third, some carnivores (in particular species with large home ranges and long daily travel distances in the wild, such as some bear species) are suggested to have more difficulties to cope with captive conditions than others, which would negatively impact animal welfare (Clubb and Mason 2007). We predicted that enrichment elicits (1)





higher use of non-used/less frequented areas within the enclosure, (2) changes in behavior, (3) changes in temporal patterns regarding enclosure space use and behavior, (4) higher activity budget, and (5) increased visibility (i.e. number of individuals visible at a moment) of animals. Furthermore, we aimed at investigating how wildlife park visitors experience the animals (among others animal visibility and enclosure design) by using a questionnaire.

Materials & Methods

Field site and study animals

This study was conducted in collaboration with the Cumberland Wildlife Park Grünau in Grünau im Almtal (Austria, 47°48°N, 13°56°E). The Wildlife Park is a popular tourist attraction in Upper Austria and houses more than 40 animal species, with around 500 animals on an area that expands over 60 ha. Here, we focused on four species: (1) brown bears (N=2, 1 adult female and 1 adult male), (2) pine martens (N=4, 1 adult female, 1 adult male, 2 juveniles), (3) domestic ferrets (N=3, 2 adult females and 1 adult male), and (4) golden jackals (N=2, 1 adult female and 1 adult male). The enclosures (approximate enclosure sizes: brown bears 5100 m², pine martens 60 m², domestic ferrets 30 m², golden jackals 900 m²) are designed to imitate natural habitats and are equipped with natural substrates, like soil, vegetation, rocks and wood. The brown bears are housed in a communal enclosure together with European wolves. Their enclosure features caves, forest sites, a pond, and access to a river. The enclosures of the brown bears and golden jackals both have open tops, allowing other animals, such as common ravens (*Corvus corax*), to enter. The other two enclosures are completely closed.

Study design

Enclosure use and behavioral data were collected from 9th September 2021 to 20th November 2021. The observation period was divided into three phases: (1) pre-enrichment (between 10 and 12 days long; baseline, no experience with the enrichment yet), (2) during enrichment (between 14 and 17 days long; enrichment was provided at locations in the enclosures that were/are low frequented but also easily visible





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to visitors), and (3) post-enrichment (between 7 and 12 days long; enrichment was removed from the enclosures). Observations were performed between 0800 AM and 0600 PM within the opening hours (1000 AM to 0400 PM) of the Wildlife Park, in three time intervals: (1) 0800 AM till 1100 AM, (2) 1100 AM till 0200 PM, and (3) 0200 PM till 0600 PM. In total, we collected 95 observations for the brown bears (31 hours and 40 minutes, pre-enrichment = 17 hours and 20 minutes, during enrichment = 12 hours and 20 minutes, post-enrichment = 2 hours; mean \pm SD observations per day = 3 ± 2), 79 observations for the pine martens (26 hours and 20 minutes, pre-enrichment = 7 hours and 20 minutes, during enrichment = 9 hours and 40 minutes, post-enrichment = 7 hours and 20 minutes; mean±SD observations per day = 2±1), 109 observations for the domestic ferrets (36 hours and 20 minutes, pre-enrichment = 5 hours and 40 minutes, during enrichment = 6 hours and 20 minutes, post-enrichment = 6 hours and 40 minutes; mean \pm SD observations per day = 2 ± 1), and 122 observations for the golden jackals (40 hours and 40 minutes, pre-enrichment = 17 hours and 20 minutes, during enrichment = 10 hours and 20 minutes, postenrichment = 13 hours; mean±SD observations per day = 3±2). Observations were performed on grouplevel. To measure animal visibility and visitor flow, observers stood at locations that were easily accessible for visitors. As the brown bear and golden jackal enclosures were too big to get an overview of the whole area from one point alone, several observation points were selected (three at the brown bears, two at the golden jackals). One observation point was sufficient at the ferrets and pine martens.

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Enrichment

The enrichment items provided to the different species were food-based (i.e. brown bear, pine marten, ferret, and golden jackal) and olfactory enrichment (i.e. golden jackal). The time and location of enrichment in the enclosure were determined after the 'pre-enrichment' phase, to adapt enrichment items to the needs of each species (i.e. according to their enclosure space use and temporal behavioral pattern observed in phase 1) and to enhance animal visibility for the visitors. The enrichment was introduced in the morning between 0800 AM and 1100 AM, either additionally to the scheduled feeding (i.e. brown bears) or outside the feeding context (i.e. golden jackal, pine marten, and ferret). During feeding, the





brown bears had to be confined in order to allow the animal caretakers to enter the enclosure and to distribute the food. To avoid additional disturbances to the animals' temporal behavior patterns (e.g. additional confinements), we decided to coordinate the enrichment procedure with the feeding schedule in the brown bear enclosure. The enrichment was renewed every second day for the brown bears, pine martens, and ferrets, and once a week for the golden jackals. The timing of enrichment presentation differed in golden jackals from that of the other species, because scent should not dissipate too quickly as long as strong scent is used.

The brown bears received two 0.5 m to 1 m long acacia logs as enrichment objects. Dried fruit, honey, yogurt and nuts were hidden in drilled holes of various sizes, which could be obtained by intensive and long-term activity. This references to bears in the wild spending about 50% of their active time with food procurement (Seryodkin et al. 2013; Schneider et al. 2014). Food procurement consists largely of collecting and consuming various small food items, in order to ultimately meet their energy needs. By using the acacia logs, a natural behavior of food gathering is stimulated, that is often lost in zoo-housed animals due to fixed feeding procedures and schedules (Grandia et al. 2001).

The pine martens and domestic ferrets were provided with a wire mesh covered wooden box measuring approximately 20 cm x 20 cm. The box was filled with pine cones, bark, leaves, moss, cranberries, nuts, raisins, mealworms, and egg shells (egg shells were only provided to the ferrets) that the animals could reach with their paws. Pine martens and domestic ferrets can find this type of food in their natural environment and resort to it to build up food stocks, especially in autumn (i.e. the period of our data collection). The plant components can also be found by both species in forest habitats (Marinis and Masseti 1995; Bodey et al. 2011).

For the golden jackal we used both food-based and olfactory enrichment. As food-based enrichment we provided hollowed out pumpkins filled with insects, such as mealworms and stick insects. Golden jackals' diet in the wild is composed of small rodents, invertebrates, reptiles, birds, and plants (mainly fruits; Markov and Lanszki 2012). A pumpkin with food inside seemed close enough as food-based item. Olfactory enrichment was included to stimulate enclosure exploration (Clark and King 2008).





We filled four jute bags (squares of about 50 cm x 50 cm) with either Przewalski horse (*Equus przewalskii*), European wolf, or rat feces (all species are housed in the Wildlife Park, the latter is used as food). The bags were randomly distributed in the enclosure and were attached to trees with twine (either on the ground or 1 m above the ground).

Measuring enclosure use and behavioral patterns

All data were collected with the software Animal Observer ((Caillaud 2016), Animal Observer v1.0, https://fosseyfund.github.io/AOToolBox/). We used scan sampling (Altmann 1974). The animals were observed over a time span of 20 minutes (randomized across species and the three time intervals), using a four minutes scan interval. Depending on species- and enclosure-size, the enclosures were divided into grids as follows: (1) 10 x 10 m grid for the brown bear enclosure, (2) 1 x 1 m grid for the domestic ferret and pine marten enclosures, and (3) 5 x 5 m grid for the golden jackal enclosure. The squares of the grid were labelled with letters and numbers. Enclosure use was recorded by marking the x,y position of each individual at the end of each scan interval (i.e. every four minutes) on the enclosure map using the app. Each x,y position was related to a square of the grid. Furthermore, behavioral data were collected: (1) temporal-behavior patterns (temporal refers to the three observational time intervals), i.e. self-maintenance and vigilance, locomotion (walking, pacing, climbing, hanging, approach/retreat), affiliative and agonistic interactions between conspecifics and heterospecifics, object and human interaction and (2) activity budget, i.e. activity in general (active, non-active). In addition, we recorded visibility (i.e. number of individuals visible at the moment of scan) and visitor flow. Visitor flow was defined as the number of people facing the enclosures (i.e. 0, <10, 10-20, >20 visitors at the enclosure).

Questionnaire

Since one of the goals of the Cumberland Wildlife Park Grünau is to enhance the visitor experience, we prepared a survey to learn about visitors' ability to experience animals in the Wildlife Park. We created an online questionnaire using Microsoft Excel online 365. From September to





November 2021, 86 visitors completed the questionnaire. Information on the participating visitor groups is summarized in Table 1. The questionnaire consisted of 21 questions (Supplementary Material, Table S1) – 12 closed questions (single choice and a five-point Likert scale from 'not important' to 'very important') and 9 open questions – and was structured into three sections: (1) information about the respondent, (2) interests of the visitors in the Cumberland Wildlife Park Grünau, (3) visitors' experience of animals at the Cumberland Wildlife Park Grünau. Here, we focus on the first and third sections of the questionnaire.

Data analysis

All analyses were performed using the software R 4.0.2 (R Core Team 2020) and the package 'mgcv' (Wood 2011). The 'post-enrichment' phase (data collected in November) was excluded from the brown bear dataset, as both brown bears were already showing signs of starting hibernation and, therefore, enclosure use and behavioral patterns were not comparable to the previous phases. Regarding the golden jackals, both individuals did not leave their burrows during daytime during the entire observation period. However, we know that the introduced enrichments were used during night, which was recorded with wildlife cameras. For this reason, no observations of golden jackals were possible, they were excluded from the statistical analysis. All other-species were analyzed in separate models.

Enclosure use. The species' extent of enclosure use was assessed using the traditional Spread of Participation Index (SPI, Dickens 1955), as we were interested in the change that enrichment elicits in enclosure use, rather than in the use of enclosure resources in general. The SPI was calculated for each combination of phase and time interval (i.e. pre-enrichment 0800 AM – 1100 AM, pre-enrichment 1100 AM – 0200 PM, pre-enrichment 0200 PM – 0600 PM, enrichment 0800 AM – 1100 AM, enrichment 1100 AM – 0200 PM, enrichment 0200 PM – 0600 PM, post-enrichment 0800 AM – 1100 AM, post-enrichment 1100 AM – 0200 PM, post-enrichment 0200 PM – 0600 PM). SPI values range from 0 (equal use of the enclosure) to 1 (unequal use of the enclosure, i.e. some enclosure zone are preferred over





others). The formula for the traditional SPI is as follows: $SPI = M(n_b - n_a) + (F_a - F_b)/2(N - M)$; where N is the total number of observations made across all enclosure zones, M is the mean number of observations made per enclosure zone, n_a is the number of zones that have a total number of observations greater than M, n_b is the number of zones that have a total number of observations less than M, F_a is the total number of observations in zones with frequencies greater than M, and F_b is the total number of observations in zones with frequencies less than M.

Temporal behavioral patterns and activity budget. To investigate whether enrichment influences temporal behavior patterns and activity budget we used a Generalized Linear Mixed Model (GLMM) with binomial error structure and logit link function. We included phase, time interval, and visitor flow as fixed factors. Originally, we included also the interaction between phase and time interval in all models. However, some models did not converge, and therefore we excluded the interaction from the model. Observation ID was added as random effect to account for the possibility that behavioral patterns varied between scan samples.

Animal Visibility. To analyze how the proportion of visible individuals varied with phase, time interval, and visitor flow we used a GLMM with binomial error structure and logit link function.

Observation ID and scan sampling ID nested in observation ID were included as random intercept. The reason for including this latter random intercept was that we had multiple scans per observation. In R such an analysis of proportions is possible by using a two-columns matrix with the number of visible and not visible individuals as the response.

As an overall test of the effect of the fixed effects we compared the full model with a null model lacking the fixed effects but otherwise being identical to the full model using a likelihood ratio test.

To rule out collinearity we determined Variance Inflation Factors (VIF) for a standard linear model excluding the random effect. No collinearity among phase, time interval and visitor flow was detected.





296	The models were fitted in R using the function glmer of the R package lme4. Tests of the individual
297	fixed effects were derived using likelihood ratio tests; R function drop1 with argument 'test' set to
298	'Chisq'.
299	Some behaviors were observed rarely (less than 5% of the total observations; e.g. affiliative and
300	human interactions for all three species, agonistic interactions for brown bears and domestic ferrets, and
301	object interactions for domestic ferrets) and where thus not included in the models.
302	
303	Results
304	Enclosure use. During enrichment, brown bears (Figure 1 B) used more zones of the enclosure in
305	the morning (SPI values: morning=0.686, midday=0.881, afternoon=0.851), as compared to pre-
306	enrichment (Figure 1 A, SPI values: morning=0.955, midday=0.812, afternoon=0.806). In contrast,
307	enrichment did not elicit a change in enclosure use in pine martens (Figure 2, SPI values: pre-enrichment
308	- morning=0.527, midday=0.532, afternoon=0.444; enrichment - morning=0.518, midday=0.530,
309	afternoon=0.496; post-enrichment - morning=0.642, midday=0.560, afternoon=0.562) and domestic
310	ferrets (Figure 3, SPI values: pre-enrichment – morning=0.567, midday=0.672, afternoon=0.612;
311	enrichment – morning=0.556, midday=0.537, afternoon=0.597; post-enrichment – morning=0.567,
312	midday=0.505, afternoon=0.672).
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314	Temporal behavioral patterns and activity budget. Overall, there was a clear impact of the fixed
315	effects phase, time interval, and visitor flow on object interaction (likelihood ratio test comparing full and
316	null model: \Box^2 =24.025, df=5, p<0.001) in brown bears. More specifically, object interaction in brown
317	bears was more frequently observed during the morning as compared to midday and afternoon (Table 2).
318	However, phase and visitor flow had no effect on object interaction. Phase, time interval, and visitor flow
319	had no obvious impact on activity (likelihood ratio test comparing full and null model: □²=10.579, df=5,
320	p=0.060), locomotion (likelihood ratio test comparing full and null model: □²=1.971, df=5, p=0.853), and
321	self-maintenance (likelihood ratio test comparing full and null model: □²=1.693, df=5, p=0.890) in brown



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In pine martens, there was an overall effect of the fixed effects phase, time interval, and visitor flow on object interaction (likelihood ratio test comparing full and null model: \(\sigma^2=19.524\), df=6, p=0.003), activity (likelihood ratio test comparing full and null model: $\Box^2=16.549$, df=6, p=0.011), locomotion (likelihood ratio test comparing full and null model: □²=35.560, df=6, p<0.001), and agonistic interaction (likelihood ratio test comparing full and null model: □²=25.307, df=6, p<0.001). Specifically, object interaction increased during enrichment and declined in the afternoon. Activity increased from pre-enrichment to enrichment and post-enrichment. Pine martens showed a higher frequency of locomotion during post-enrichment than during the other two phases. Furthermore, agonistic interactions were less frequently observed during post-enrichment compared to the other phases, and less agonistic interactions occurred when less than 10 visitors were watching the enclosure as compared to 0 and 10-20 visitors (Table 2). There was no obvious difference between time intervals and visitor flow with regard to activity and locomotion, and agonistic interactions did not differ between time intervals. The fixed factors phase, time interval, and visitor flow had no effect on self-maintenance (likelihood ratio test comparing full and null model: $\Box^2=2.689$, df=6, p=0.847) in pine martens. Phase, time interval, and visitor flow had no obvious impact on activity (likelihood ratio test comparing full and null model: $\Box^2=7.048$, df=5, p=0.217), locomotion (likelihood ratio test comparing

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full and null model: \Box^2 =4.534, df=5, p=0.475), and self-maintenance (likelihood ratio test comparing full

and null model: $\Box^2=9.809$, df=5, p=0.081) in domestic ferrets.

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Visibility. In brown bears, there was an overall effect of phase, time interval, and visitor flow on the number of individuals visible at the moment of scan (likelihood ratio test comparing full and null model: $\Box^2=17.177$, df=5, p=0.004). Visibility increased with the number of visitors (Table 3). Phase, time interval, and visitor flow had no obvious effect on the visibility of domestic ferrets (likelihood ratio test comparing full and null model: $\Box^2=8.323$, df=5, p=0.139) and pine martens (likelihood ratio test comparing full and null model: $\Box^2=9.009$, df=6, p=0.173).

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Questionnaire. More than 90% of the visitors (79 visitors at the brown bear enclosure and 80 visitors at the golden jackal enclosure) reported that they like the enclosures of the brown bear and golden jackal (Figures 4 and 5). However, only 48% (41 visitors at the domestic ferret enclosure) and 56% (48 visitors at the pine marten enclosure) reported that they like the domestic ferret and pine marten enclosures (Figures 6 and 7). Similarly, the majority of the visitors reported that the brown bear and golden jackal enclosures look natural, but far fewer shared this opinion for the other two enclosures (brown bear: 76 visitors – 88%, golden jackal: 76 visitors – 88%, domestic ferret: 37 visitors – 43%, pine marten: 42 visitors – 49%).

In more than 60% of the cases, visitors reported enough resting places inside the enclosures (brown

bear: 75 visitors – 87%, golden jackal: 53 visitors – 62%, domestic ferret: 63 visitors – 73%, pine marten: 68 visitors – 79%, Figures 4-7). Fifty-nine visitors (69%) reported that the brown bear enclosure offers enough space for the animals, but less than half of the visitors reported that case for the golden jackal (40 visitors – 47%), domestic ferret (29 visitors – 34%) and pine marten (33 visitors – 38%) enclosures. A good share of visitors, however, just does not know. Furthermore, the visitors were not convinced that the enclosures provide enough opportunities/stimulations for activity for the animals (brown bear: 43 visitors – 50%, golden jackal: 30 visitors – 35%, domestic ferret: 31 visitors – 36%, pine marten: 43 visitors – 50%). But, almost as many visitors reported that they do not know whether the enclosures provide enough stimulation for activity.

Most visitors, who completed the questionnaire, reported that they have seen the brown bears (62 visitors – 72%, Figure 4) and pine martens (66 visitors – 77%, Figure 6) being active, while the golden jackals (12 visitors – 14%, Figure 5) and domestic ferrets (35 visitors – 41%, Figure 7) were rarely observed.

Discussion

Our results of testing the effect of enrichment in three zoo-housed mammalian species partially



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support the assumption that enrichment elicits a change in enclosure use and behavioral patterns. However, with a small sample size and the fact that not all effects were found in all species, these results need to be interpreted with caution. First, as expected, enrichment induces a more uniform use of the enclosure in brown bears. However, it had no effect on the use of enclosure space in the other species, i.e. pine martens, domestic ferrets, and golden jackals. Second, object interaction, activity in general, and locomotion in pine martens increased from pre-enrichment to the enrichment phase. Third, visibility in brown bears did not increase with enrichment, but rather with the number of visitors. Furthermore, more than half of the interviewed visitors reported that the brown bear, golden jackal, and pine marten enclosures look natural, while the enclosure of the domestic ferret would benefit from changes in design. Enrichment resulted in a more homogeneous use of enclosure zones in brown bears, while no effect was apparent in the other three species. The change in enclosure use in brown bears as a result of enrichment is consistent with the findings described for various other species (brown bears, Soriano et al. 2015; kinkajous *Potos flavus*, Blount and Taylor 2000; fishing cats *Felis viverrina*, Shepherdson et al. 1993). Captive carnivores often show low activity and enclosure use due to inadequate feeding conditions (Bashaw et al. 2003), encouraging the inclusion of food-based or other types of enrichments. In the present study, a difference in enclosure use was only apparent in the morning (0800 AM till 1100 AM) when the food-based enrichment was freshly placed inside the enclosure. As the acacia logs filled with food were presented only every second day in the morning, a prolonged and more frequent presentation of the enrichment, as well as more frequent changes in location and selection of various hiding places, might enhance the effect and maintain the desired change in a uniform use of different zones over time. Although, in captivity, some carnivorous species also seem to adapt better to housing conditions than other species, which is related to their small home range size and short daily travel distance (Clubb and Mason 2007). Unsuitable type or location and quantity of enrichment may affect the successful implementation of enrichment (Weerd and Ison 2019), which may have been the reason that domestic ferrets and pine martens did not change their enclosure use. While the pine martens at least manipulated and inspected the





food-based enrichment, the domestic ferrets showed little interest in it. This suggests that the type of enrichment was unsuitable for the domestic ferrets. Different objects that can be used for climbing or digging boxes (e.g. boxes filled with rice in which small objects are hidden) could increase their interest. The golden jackals in the current study responded to olfactory and food-based enrichment only during night and were not visible at all during the observation period. Even though their wild counterparts show higher activity patterns during night, diurnal movements occur on a smaller scale (Fenton et al. 2021). However, the type of olfactory and food-based enrichment used may not have been the adequate type of enrichment to change the activity patterns of this carnivorous species to diurnal rhythms. In particular, the choice of scent seems to play an important role as not all scents achieve the desired goals and in some cases can even increase inactivity (Clark and King 2008). We used semi-concentrated scents in jute bags, which may have caused the scent to dissipate too quickly, causing the animals to lose interest. In this respect, electronic feeders delivering food unpredictably in time rather than conventional feeding seem to enhance activity (Kistler et al. 2009), suggesting that the unpredictability and the need to search for food may be better suited to elicit a change in activity patterns in golden jackals.

Object interaction, activity in general, and locomotion in pine martens was altered due to food-based enrichment. Enrichment with extrinsic reinforcement (such as food) seem to procure better and more prolonged behavioral changes than ones with intrinsic reinforcements (i.e. behavior itself; Tarou and Bashaw 2007). The food-based enrichments used in the current study did not seem to be effective in the same way for all study species. However, the timing of food-based enrichment was rather predictable (i.e. the objects were always placed inside the enclosures at approximately the same time), which may be a reason why the enrichment was not an overall success. Activity rhythms are highly modifiable with food availability (Boulos and Terman 1980; Ware et al. 2012). The activity of pine martens in the wild, for instance, changes seasonally and tends to be bimodal in autumn (Zalewski 2001). Similarly, captive brown bears are mainly diurnal with a strong crepuscular component (Ware et al. 2012) as compared to their wild counterparts, which exhibit nocturnal behavior (Kaczensky et al. 2006). Therefore, the activity in this study is consistent with the activity pattern of other captive bears, but diverges greatly from that of



426 animals living in the wild. Still, enrichment can contribute to improved welfare of the animals as it can 427 reduce stress of zoo-housed/captive animals (Hansen and Berthelsen 2000; McDougall et al. 2006; 428 Poessel et al. 2011) and not species-typical inactivity would imply stereotypy (Renner and Lussier 2002). 429 Furthermore, habituation can also influence the effectiveness of enrichment, which emphasizes that 430 enrichment should be slightly adapted each time of presentation to induce animals to use the enrichment 431 for longer periods (Tarou and Bashaw 2007). 432 Contrary to expectations, enrichment did not enhance visibility of animals. But, for brown bears, 433 visibility increased with the number of visitors in front of the enclosure. This suggests that visitors can 434 also act as a form of enrichment for captive animals (Rault et al. 2020). Visitors can have positive (Bloomfield et al. 2015; Hashmi and Sullivan 2020), neutral (Sherwen et al. 2014) or negative (Davis et 435 436 al. 2005; Hashmi and Sullivan 2020; Larsen et al. 2014) impacts on zoo-housed animals, depending on 437 the type of visual or acoustic interactions with the animals. For instance, meerkats (Suricata suricatta) 438 showed fewer social interactions during the zoo closure due to COVID-19 pandemic than during times 439 when visitors were allowed back into the zoos (Williams et al. 2021). However, this effect probably also 440 depends on the propensity of the animals to interact with humans, which may explain the discrepancy 441 found between species in the current study. Various bear species (e.g. sloth bears *Melursus ursinus*, 442 Andean bears Tremarctos ornatus, grizzly bears Ursus arctos horribilis, American black bears Ursus 443 americanus, Malayan sun bear Helarctos malayanus) seem to be more visible in the presence of visitors 444 (Bernstein-Kurtycz et al. 2021), while other species seem to show avoidance behavior (e.g. quokkas 445 Setonix brachyurus, Learmonth et al. 2018; orangutans Pongo pygmaeus, Birke 2002; jaguars Panthera 446 onca, Sellinger and Ha 2005). 447 According to our questionnaire visitors perceived brown bears, golden jackals, and pine martens to have the most natural enclosures. However, less than half of the visitors reported the domestic ferret 448 449 enclosure as resembling the natural environment. This low natural appearance may also be a reason for 450 the lack of change in enclosure use and behavioral diversity observed in the domestic ferrets. Natural 451 living conditions and the optimum animal welfare in zoological institutions are difficult to assess as not





all natural enclosure designs benefit captive animals (Learmonth 2019). The Cumberland Wildlife Park Grünau counts approximately 100,000 visitors per year. Thus, with a small sample size of 86 visitors completing the questionnaire, eaution must be applied, as the findings might not be representative. Still, the survey results of the current study clearly show that visitors value animal welfare and natural enclosure design. Similarly, visitors of the Córdoba Zoo considered capybaras (*Hydrochoerus hydrochaeris*) in the wild to have the most animal welfare compared to zoo-housed individuals (Chiapero et al. 2021). Thus, designing enclosures matching the natural habitat, as well as introducing environmental enrichments is valuable to maintain visitor interest, but also to promote education – on animal welfare, environmental awareness, wildlife conservation, and human-wildlife conflicts – as it stimulates visitors to read the enclosure signage.

Conclusion

Although this study shows some findings that may suggest that food-based enrichment can, to some extent, elicit a change in enclosure use and enhance behavioral diversity in captive carnivore species, these results should be interpreted with caution due to the small sample size and inconsistent results. The results indicate the importance of evaluating long-term effects of enrichment, as not all species reacted to the enrichment and no prolonged changes in enclosure use or behavior were observed. Furthermore, before introducing enrichments, it is important to consider whether the type of enrichment is suitable to achieve the desired goal and does not foster undesired behavior. Thus, testing species-specific preferences of environmental enrichment prior to integrating and presenting them in the enclosures, as well as testing their effect on enclosure use and behavioral diversity, is crucial. Furthermore, involving zoo visitors in decision-making processes about animal enclosure design and consequently animal welfare, could raise awareness of nature and promote education.





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Figure labels

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649	Figure 1. Brown bear enclosure use. The extent of enclosure use pre-enrichment (A) and during
650	enrichment (B) is shown on a scale (density level) from white (low) to red (high) for each square of the
651	10x10 m grid and divided into three time intervals. Enclosure use indicates the total number of sightings
652	of individuals in a specific sector independent of activity level. Point size increases with activity level (i.e.
653	total number of sightings of active animals in a specific sector of the enclosure) per square. Enclosures
654	labelled with '1' is accessible for brown bears and European wolves. Enclosure labelled with '2' is only
655	accessible for the European wolves.
656	
657	Figure 2. Pine marten enclosure use. The extent of enclosure utilization pre-enrichment (A), during
658	enrichment (B), and post-enrichment (C) is shown on a scale (density level) from white (low) to red
659	(high) for each square of the 10x10 m grid and divided into three time intervals. Enclosure use indicates
660	the total number of sightings of individuals in a specific sector independent of activity level. Point size
661	increases with activity level (i.e. total number of sightings of active animals in a specific sector of the
662	enclosure) per square.
663	
664	Figure 3. Domestic ferret enclosure use. The extent of enclosure utilization pre-enrichment (A), during
665	enrichment (B), and post-enrichment (C) is shown on a scale (density level) from white (low) to red
666	(high) for each square of the 10x10 m grid and divided into three time intervals. Enclosure use indicates
667	the total number of sightings of individuals in a specific sector independent of activity level. Point size
668	increases with activity level (i.e. total number of sightings of active animals in a specific sector of the
669	enclosure) per square.
670	
671	Figure 4. Responses to the brown bear enclosure of the third section of the questionnaire in percent.
672	
673	Figure 5. Responses to the golden jackal enclosure of the third section of the questionnaire in percent.



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674	
675	Figure 6. Responses to the pine marten enclosure of the third section of the questionnaire in percent.
676	
677	Figure 7. Responses to the domestic ferret enclosure of the third section of the questionnaire in percent.
678	
679	



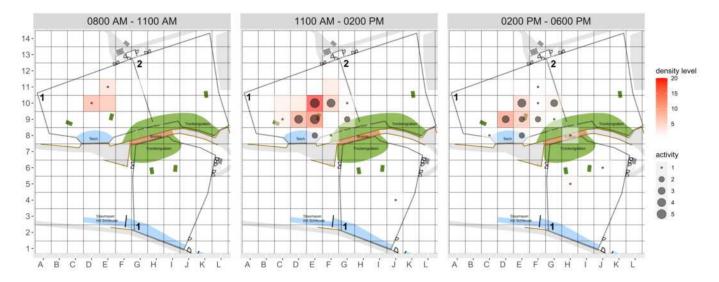
Figure 1

Figure 1. Brown bear enclosure use.

The extent of enclosure use pre-enrichment (A) and during enrichment (B) is shown on a scale (density level) from white (low) to red (high) for each square of the 10x10 m grid and divided into three time intervals. Enclosure use indicates the total number of sightings of individuals in a specific sector independent of activity level. Point size increases with activity level (i.e. total number of sightings of active animals in a specific sector of the enclosure) per square. Enclosures labelled with '1' is accessible for brown bears and European wolves. Enclosure labelled with '2' is only accessible for the European wolves.



Α



В

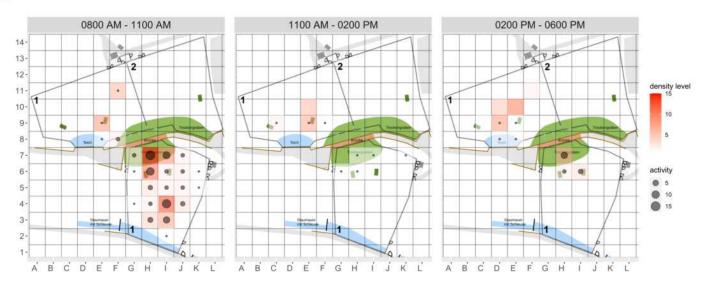


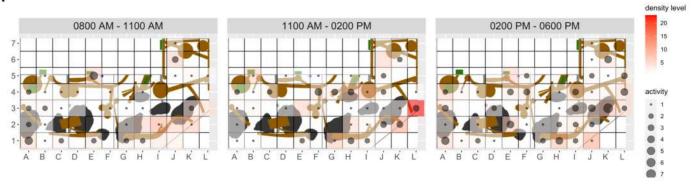


Figure 2. Pine marten enclosure use.

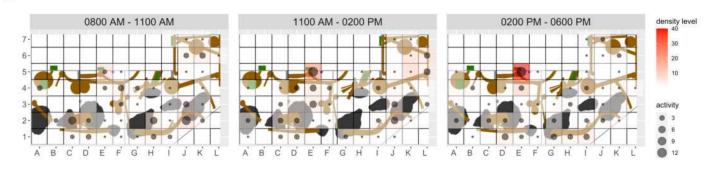
The extent of enclosure utilization pre-enrichment (A), during enrichment (B), and post-enrichment (C) is shown on a scale (density level) from white (low) to red (high) for each square of the 10x10 m grid and divided into three time intervals. Enclosure use indicates the total number of sightings of individuals in a specific sector independent of activity level. Point size increases with activity level (i.e. total number of sightings of active animals in a specific sector of the enclosure) per square.







В



C

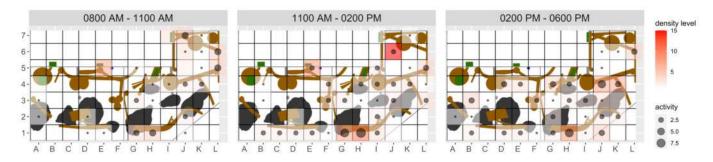


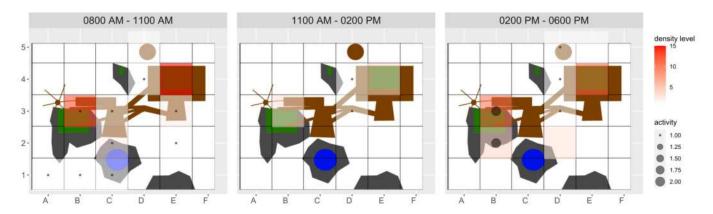


Figure 3. Domestic ferret enclosure use.

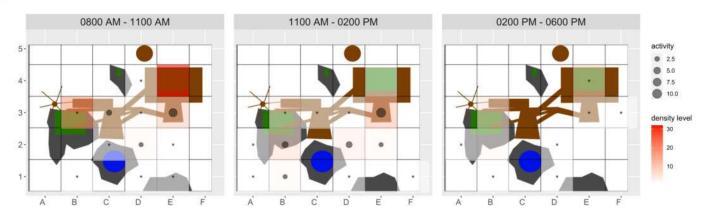
The extent of enclosure utilization pre-enrichment (A), during enrichment (B), and post-enrichment (C) is shown on a scale (density level) from white (low) to red (high) for each square of the 10x10 m grid and divided into three time intervals. Enclosure use indicates the total number of sightings of individuals in a specific sector independent of activity level. Point size increases with activity level (i.e. total number of sightings of active animals in a specific sector of the enclosure) per square.



Α



В



C

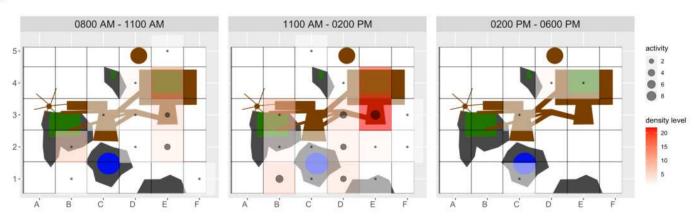




Figure 4. Responses to the brown bear enclosure of the third section of the questionnaire in percent.

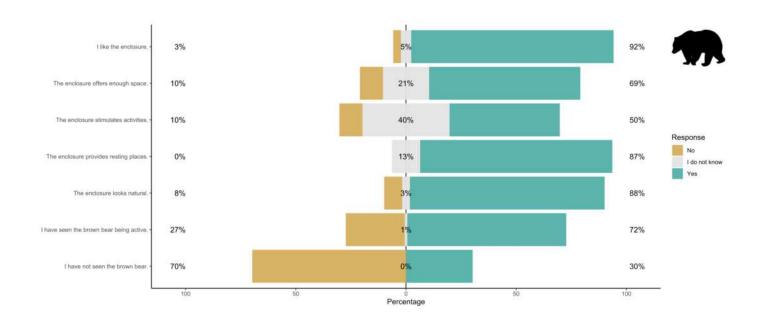




Figure 5. Responses to the golden jackal enclosure of the third section of the questionnaire in percent.

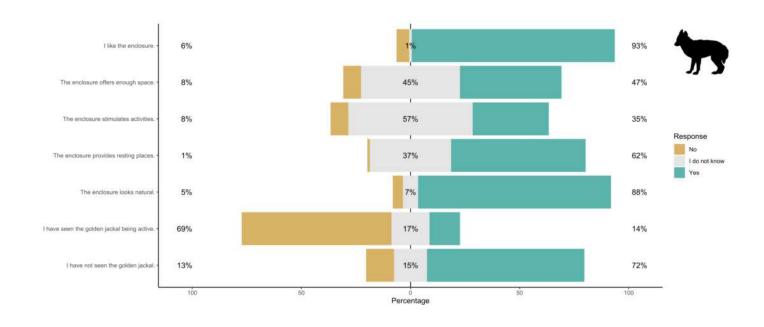




Figure 6. Responses to the pine marten enclosure of the third section of the questionnaire in percent.

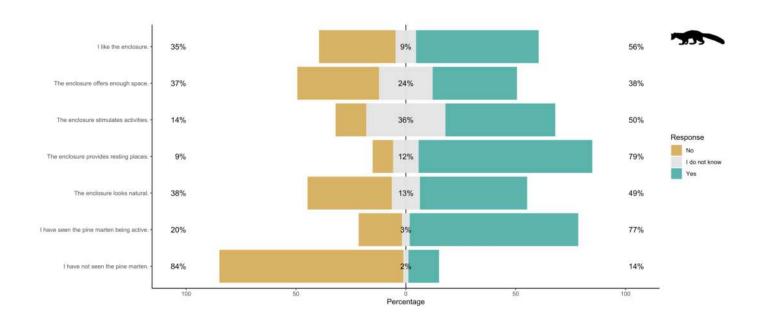




Figure 7. Responses to the domestic ferret enclosure of the third section of the questionnaire in percent.

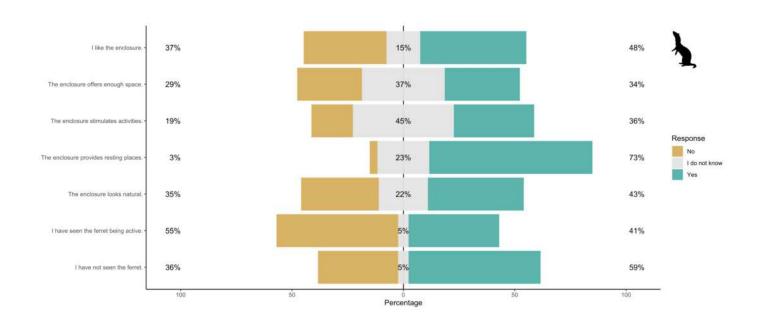




Table 1(on next page)

Table 1. Descriptive statistics of questionnaire participants.



1 Table 1. Descriptive statistics of questionnaire participants.

Personal information	N=86	%	
Age	Younger than 15	8	9.3
	15-24	17	19.8
	25-64	61	70.9
	65 or older	0	0.0
Gender	Female	50	58.1
	Male	36	41.9
	Other	0	0.0
	I prefer not to say	0	0.0
Education: level completed	Compulsory school	27	32.1
	Higher school	24	28.6
	Studies	33	39.3
Visitation to wildlife	Regularly (once a month)	16	18.6
parks/zoos			
	Often (once every few months)	45	52.3
	Sometimes (once a year)	18	20.9
	Rarely (once every few years)	7	8.1
Visitation with whom	Alone	5	5.8
	Two or more, without children <12	34	39.5
	Two or more, with children <12	41	47.7
	School class	1	1.2
	Other group	5	5.8



Table 2(on next page)

Table 2. Results of the behavioral pattern models.

Estimates, together with standard errors (SE), confidence intervals (lower and upper CI), significance tests as well as minimum and maximum of model estimates obtained when excluding individual terms one at a time are given.



- 1 Table 2. Results of the behavioral pattern models. Estimates, together with standard errors (SE),
- 2 confidence intervals (lower and upper CI), significance tests as well as minimum and maximum of model
- 3 estimates obtained when excluding individual terms one at a time are given.

term	estimate	SE	lower	upper	2	df	p	min	Max
			CI	CI					
Brown bear ob	ject intera	ction							
intercept	-1.604	1.037	-18.214	0.572			(1)	-2.534	-0.341
phase (during	0.955	1.021	-1.235	17.535	0.827	1	0.363	-0.241	1.911
enrichment)(2)									
time interval	-2.424	1.065	-64.351	-0.900	15.069	2	0.001	-3.128	-1.838
(1100 AM –									
0200 PM) ⁽³⁾									
time interval	-3.655	1.206	-74.415	-2.017				-22.912	-3.389
(0200 PM –									
0600 PM) ⁽³⁾									
visitor flow	-0.808	0.878	-13.350	0.904	1.569	2	0.456	-1.245	-0.314
(<10)(4)									
visitor flow	0.516	0.759	-1.196	2.127				0.085	0.866
(10-20)(4)									
Pine marten ac	tivity								
intercept	0.677	0.494	-0.275	1.686			(1)	0.488	0.949
phase (during	1.632	0.516	0.713	2.660	12.455	2	0.002	1.460	1.787
enrichment)(2)									
phase (post-	1.694	0.557	0.572	2.788				1.518	1.835
enrichment)(2)									



time interval	-0.801	0.453	-1.708	0.052	4.104	2	0.128	-1.319	-0.706
(1100 AM –									
0200 PM) ⁽³⁾									
time interval	-0.010	0.537	-1.027	1.089				-0.290	0.162
(0200 PM –									
0600 PM) ⁽³⁾									
ŕ									
visitor flow	-0.165	0.230	-0.627	0.288	0.568	2	0.753	-0.266	-0.046
(<10) ⁽⁴⁾									
visitor flow	0.190	1.014	-1.665	12.760				-1.277	1.295
(10-20)(4)									
Pine marten loc	comotion								
intercept	-1.272	0.318	-1.910	-0.670			(1)	-1.389	-1.112
phase (during	0.185	0.306	-0.418	0.762	32.104	2	<0.001	0.026	0.296
enrichment)(2)									
phase (post-	1.805	0.336	1.204	2.492				1.708	1.909
enrichment)(2)									
time interval	-0.070	0.296	-0.632	0.562	2.837	2	0.242	-0.193	-0.003
(1100 AM –									
0200 PM) ⁽³⁾									
time interval	0.402	0.316	-0.212	1.034				0.296	0.475
(0200 PM –									
0600 PM) ⁽³⁾									
visitor flow	-0.116	0.197	-0.529	0.263	0.835	2	0.659	-0.184	-0.033
(<10)(4)									
								l l	



(10-20)(4)									
Pine marten ag	onistic inte	raction							
intercept	-2.255	0.563	-3.489	-1.320			(1)	-2.587	-2.110
phase (during	0.414	0.539	-0.668	1.515	8.871	2	0.012	0.254	0.670
enrichment)(2)									
phase (post-	-1.401	0.674	-3.154	-0.093				-1.755	-1.108
enrichment) ⁽²⁾									
time interval	-0.760	0.525	-1.857	0.303	2.131	2	0.345	-0.933	-0.567
(1100 AM –									
0200 PM) ⁽³⁾									
time interval	-0.478	0.557	-1.689	0.687				-0.733	-0.262
(0200 PM –									
0600 PM) ⁽³⁾									
visitor flow	-1.485	0.422	-2.597	-0.739	17.061	2	<0.001	-2.291	-1.220
(<10) ⁽⁴⁾									
visitor flow	1.063	0.986	-19.019	3.079				-13.784	2.968
(10-20) ⁽⁴⁾									
Pine marten ob	ject interac	ction							
intercept	-4.923	0.989	-18.442	-3.325			(1)	-5.451	-4.632
phase (during	3.539	0.903	1.958	16.923	17.164	2	< 0.001	3.306	4.128
enrichment)(2)									
phase (post-	0.300	1.180	-14.051	13.874				-0.479	0.997
enrichment)(2)									
time interval	-1.382	0.788	-3.085	0.217	4.764	2	0.092	-1.702	-1.173
(1100 AM –									



0200 PM) ⁽³⁾									
time interval	-1.918	0.878	-4.097	-0.206				-2.423	-1.706
(0200 PM –									
0600 PM) ⁽³⁾									
visitor flow	0.271	0.418	-0.550	1.121	0.632	2	0.729	0.107	0.400
(<10) ⁽⁴⁾									
visitor flow	-12.903	323.817	-16.060	-8.563				-14.419	-11.960
(10-20)(4)									

- 4 (1)not indicated because of having a very limited interpretation
- 5 (2)dummy coded with pre-enrichment being the reference category
- 6 (3)dummy coded with the time interval from 0800 AM till 1100 AM being the reference category
- 7 (4)dummy coded with 0 visitors being the reference category

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Table 3(on next page)

Table 3. Results of the visibility model.

Estimates, together with standard errors (SE), confidence intervals (lower and upper CI), significance tests as well as minimum and maximum of model estimates obtained when excluding individual terms one at a time are given.



- 1 Table 3. Results of the visibility model. Estimates, together with standard errors (SE), confidence
- 2 intervals (lower and upper CI), significance tests as well as minimum and maximum of model estimates
- 3 obtained when excluding individual terms one at a time are given.

term	estimate	SE	lower	upper		df	p	min	Max
			CI	CI					
Brown bear v	isibility								
intercept	-2.592	1.311	-6.206	-0.305			(1)	-3.222	-2.123
phase (during enrichment) ⁽²⁾	1.682	1.215	-0.574	4.720	2.025	1	0.155	1.259	2.079
time interval (1100 AM – 0200 PM) ⁽³⁾	-1.750	1.395	-5.115	0.626	1.671	2	0.434	-2.215	-1.283
time interval (0200 PM – 0600 PM) ⁽³⁾	-0.517	1.447	-3.929	2.670				-0.946	-0.048
visitor flow (<10) ⁽⁴⁾	1.223	0.404	0.433	2.112	13.479	2	0.001	0.924	1.433
visitor flow (10-20) ⁽⁴⁾	2.180	0.860	0.327	4.436				1.744	3.291

- 4 (1)not indicated because of having a very limited interpretation
- 5 (2)dummy coded with pre-enrichment being the reference category
- 6 (3)dummy coded with the time interval from 0800 AM till 1100 AM being the reference category
- 7 (4)dummy coded with 0 visitors being the reference category

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