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

First revision

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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 (food-based or non-food-based items, such as environmental, sensory, cognitive, social) 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) 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. 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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26   **Abstract**

27   **Background.** Combining naturalistic enclosure design and animal welfare with visitor interests and

28   education can be challenging for zoos and wildlife parks. To accomplish both purposes, different types of

29   enrichment (food-based or non-food-based items, such as environmental, sensory, cognitive, social) can

30   be used. The aim of the present study is to investigate the effect of food-based and olfactory enrichments

31   on enclosure use, behavior, and visibility of captive brown bears (*Ursus arctos*), pine martens (*Martes*

32   *martes*), domestic ferrets (*Mustela putorius furo*), and golden jackals (*Canis aureus*).

33   **Methods.** We used observational approaches to measure enclosure use, behavior, and visibility

34   during three different experimental phases: (1) pre-enrichment (baseline, no experience with the

35   enrichment yet), (2) during enrichment (enrichment was provided at low frequented locations in the

36   enclosures that are easily visible to visitors), and (3) post-enrichment (enrichment was removed from the

37   enclosures). In addition, visitors' perception of animal visibility and enclosure design was examined using

38   a questionnaire.

39   **Results.** We found that enrichment led to a uniform use of the enclosure and enhanced visibility in

40   brown bears, increased activity budgets in pine martens, and high object interaction in both species. No

41   effects of enrichment were observed in domestic ferrets. Golden jackals did not leave their burrows

42   during daytime during the entire observation period; thus, observations were not possible at all.

43   Furthermore, questionnaires from 86 participants showed that visitors experience enclosures very

44   differently. The visitors generally reported enough resting places, appreciated the brown bear and golden

45   jackal enclosures, and the majority rated the enclosures as natural. But, they also perceived a lack of

46   enclosure space for the pine martens, domestic ferrets, and golden jackals, as well as a lack of stimulation

47   for activity in general. Our results may indicate that food-based enrichment can affect enclosure use,

48   temporal activity patterns, and animal visibility. This may suggest that food-based-enrichment may need

49   to be selected on a species-specific basis in order to have a positive impact on the welfare of captive

50   animals.

51   **Keywords:** animal visibility, brown bear, domestic ferret, pine marten, animal welfare

52

Introduction

53

54   In captivity, enclosures often lack biological and ecological conditions that can be found in the

55   natural habitat of the animals. For instance, zoo-housed animals frequently have less space available than

56   they would use in the wild and lack enclosure complexity, which are both correlated with negative

57   welfare indices, such as stereotypies (Carlstead, 1998; Clubb & Mason, 2003; Rose et al., 2017; Mellor et

58   al., 2018). Among other approaches, environmental enrichment is most commonly used to reduce and

59   prevent the development of abnormal behaviors, to stimulate activity, and to enhance quality of life for

60   the animals (Newberry, 1995; Mellen & Sevenich MacPhee, 2001; Mason et al., 2007; Fernandez, 2022).

61   Enrichments are classified into non-food-based items, such as environmental (e.g. water element,

62   climbing structure), sensory (e.g. mirrors, scratch poles), cognitive (e.g. novel object, puzzle feeder), or

63   social (e.g. conspecifics, mixed species enclosures, human-animal interactions) stimuli, and food-based

64   items (Swaisgood & Shepherdson, 2005). However, enrichment is not only the stimulus/event, but also

65   the interaction between the stimulus/event and a positive welfare change, such as improved behavior

66   (Fernandez, 2022). While examinations of environmental enrichment are not necessarily novel, there have

67   been few empirical investigations into the effects prior to, during and after the introduction of enrichment.

68   Enrichment can stimulate animals' activities in previously underused enclosure areas, thereby

69   allowing an efficient use of the available space and promoting the uniform use of different zones (Renner

70   & Lussier, 2002; Lawrence et al., 2021). As different zones should serve different purposes – e.g.

71   sleeping, feeding, bathing, reproduction, etc. – all zones should be used by the animals. Consequently,

72   unused zones would be considered inadequate or of limited value (de Azevedo et al., 2023). For instance,

73   brown bears (*Ursus arctos*; Soriano et al., 2015) and Indian Leopards (*Panthera pardus;* Mallapur et al.,

74   2010) showed a higher use of environmentally enriched zones within their enclosure during enrichment,

75   and thereby increased the use of certain areas, rather than using only a few of them. Similar findings were

76   found in Asiatic lions (*Panthera leo persica*), which showed uniform enclosure use post-enrichment

77   (Goswami et al., 2021). The extent to which the space of an enclosure is used is considered an indicator

78 for the animal's welfare, as a non-uniform use of the enclosure could be related to inappropriate design

79 (Ross et al., 2009). Naturalistic environments reflect the respective home range size in the wild and offer

80 hiding places for the animals, which is often accompanied by low animal visibility for the visitors

81 (Bitgood et al., 1988). By contrast, other studies claim that enrichment increases the visibility of captive

82 animals (Foerder et al., 2020). Both aspects, i.e. high animal visibility and the possibility of observing a

83 species' behaviors (e.g. social interactions, locomotion, grooming) fosters and maintains visitor interest

84 (Bitgood et al., 1988; Kirchgessner & Sewall, 2015) and thus can promote public education, enable

85 research and conservation efforts (Fernandez et al., 2009; Kuhar et al., 2010).

86   In order to stimulate natural species-typical behavioral patterns, both the type and the timing when

87 an enrichment is introduced are important (Kuczaj et al., 2002). In fact, zoo-housed animals often show

88 very different behavioral patterns in comparison with individuals of the same species living in the wild

89 (Schneider et al., 2014; Inoue & Shimada, 2020). For instance, explorative behavior related to acquisition

90 and consumption of food might be remarkably absent in zoos. Western lowland gorillas (*Gorilla gorilla*

91 *gorilla*) in human care increased their activity budget reminiscent of individuals observed in the wild

92 when feeding schedules varied, rather than providing food at fixed times (Charmoy et al., 2015). Similar

93 findings were reported for cheetahs (*Acinonyx jubatus*), when feeding schedules, feeding locations, and

94 olfactory enrichment varied (Quirke & Riordan, 2011). Determining temporal behavior patterns and

95 activity budgets in captivity is particularly relevant for species that would allocate most of their active

96 time to food procurement in the wild.

97   In addition, the diversity of the natural behavioral repertoire displayed by a species in captivity may

98 increase when introducing enrichment to the enclosure (Swaisgood & Shepherdson, 2005; McPhee &

99 Carlstead, 2010). Spectacled bears (*Tremarctos ornatus*) displayed more behaviors similar to their wild

100 counterparts after introducing climbing structures and other environmental items (Renner & Lussier,

101 2002) and stereotypic behavior decreased during the introduction of enrichment as compared to pre- and

102 post-enrichment in captive sun bears (*Helarctus malayanus*; Abdul-Mawah et al., 2022) Furthermore,

103 forms of food-based enrichment, including the use of novel objects to increase the difficulty and time to

104 acquire food, can positively affect the behavioral repertoire of captive animals. Kodiak (*Ursus arctos*

105 *middendorffi*), polar (*Ursus maritimus*), and Asiatic black bears (*Ursus thibetanus*) were provided with

106 ice treats (i.e. ice blocks filled with food), which resulted in higher activity and reduced presence of

107 abnormal behavior during enrichment sessions (Forthman et al., 1992). Furthermore, when European

108 wolves (*Canis lupus lupus*) were exposed to food hidden in pouches or plastic food balls in the enclosure,

109 stereotypic behaviors and negative social behaviors decreased, and they exhibited more exploratory

110 behavior (Riggio et al., 2019). Lack of space or lack of enrichment may have detrimental effects on

111 animal behavior, such as fewer social interactions (e.g. chimpanzees (*Pan troglodytes*), Koyama &

112 Aureli, 2019) or even the occurrence of stereotypic behaviors (e.g. carnivores, ungulates, rodents, and

113 primates, Mason et al., 2007; chickens (*Gallus gallus*), Dixon et al., 2010). Natural species-specific

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

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

116 'unhappy' or 'unhealthy' (McPhee & Carlstead, 2010), which could have a negative impact on the

117 educational message of the zoo (Fernandez et al., 2009; Godinez & Fernandez, 2019). Thus, displaying

118 natural species-typical behaviors is not only crucial for animal welfare, but also for the zoo management

119 in order to maintain visitors' interest and satisfaction (McPhee & Carlstead, 2010).

120   The aim of this study was to determine the effect of enrichment (food-based and sensory items, i.e.

121 olfactory) on enclosure use, behavior and visibility (i.e. number of individuals visible at a moment) of

122 four carnivorous mammalian species in human care in a wildlife park setting: brown bears (*Ursus arctos*),

123 pine martens (*Martes martes*), domestic ferrets (*Mustela putorius furo*), and golden jackals (*Canis*

124 *aureus*). Several reasons supported the choice of these four species, which was taken in coordination with

125 the Wildlife Park management: first, all four species showed little and non-uniform use of enclosure

126 space; second, visibility of the individuals was low in two of the enclosures (i.e. golden jackals and

127 ferrets; Cumberland Wildlife Park, personal communication); and third, some carnivores (in particular

128 species with large home ranges and long daily travel distances in the wild, such as some bear species) are

129 suggested to have more difficulties to cope with captive conditions than others, which would negatively

130   impact animal welfare (Clubb & Mason, 2007). We predicted that enrichment elicits (1) higher use of

131   non-used/less frequented areas within the enclosure, (2) changes in behavior, (3) changes in temporal

132   patterns regarding enclosure space use and behavior, (4) higher activity budget, (5) increased visibility

133   (i.e. number of individuals visible at a moment) of animals, and (6) that the changes from prediction 1 to

134   5 elicited by enrichment are still present in the post-enrichment phase, albeit at a lower intensity.

135

136   ## Materials & Methods

137   **Ethical statement**

138   This study complies with all current Austrian laws and regulations concerning the work with

139   captive wildlife. All data were collected non-invasively under Animal Experiment Licence Nr. GZ2021-

140   0.873.421 by the Austrian Federal Ministry for Science and Research. The authors adhere to the

141   'Guidelines for the use of animals in research' as published in Animal Behaviour (1991, 41, 183–186).

142   We confirm that the owner of the land, the Duke of Cumberland, gave permission to conduct behavioural

143   studies on his site. A partnership agreement was signed between the research institution (KLF) and the

144   Cumberland Game Park stating the possibility of doing research with captive animals.

145   **Field site and study animals**

146   This study was conducted in collaboration with the Cumberland Wildlife Park Grünau in Grünau

147   im Almtal (Austria, 47°48'N, 13°56'E). The Wildlife Park is a popular tourist attraction in Upper Austria

148   and houses more than 40 animal species, with around 500 animals on an area that expands over 60 ha.

149   Here, we focused on four species: (1) brown bears (N=2, 1 adult female and 1 adult male), (2) pine

150   martens (N=4, 1 adult female, 1 adult male, 2 juveniles), (3) domestic ferrets (N=3, 2 adult females and 1

151   adult male), and (4) golden jackals (N=2, 1 adult female and 1 adult male). The enclosures (approximate

152   enclosure sizes: brown bears 5100 m², pine martens 60 m², domestic ferrets 30 m², golden jackals 900 m²)

153   are designed to imitate natural habitats and are equipped with natural substrates, like soil, vegetation,

154   rocks and wood. The brown bears are housed in a communal enclosure together with European wolves.

155   Their enclosure features caves, forest sites, a pond, and access to a river. The enclosures of the brown

156   bears and golden jackals both have open tops, allowing other animals, such as common ravens (*Corvus*

157   *corax*), to enter. The other two enclosures are completely closed.

158   **Study design**

159   Enclosure use and behavioral data were collected from 9th September 2021 to 20th November 2021.

160   The observation period was divided into three phases: (1) pre-enrichment (between 10 and 12 days long;

161   baseline, no experience with the enrichment yet), (2) during enrichment (between 14 and 17 days long;

162   enrichment was provided at locations in the enclosures that were/are low frequented but also easily visible

163   to visitors), and (3) post-enrichment (between 7 and 12 days long; enrichment was removed from the

164   enclosures). The length of the phases varied between species, because of different enrichment

165   implementations adapted for each species and in order to collect a similar number of observations

166   between all phases (due to restrictions in animal keepers and observer availability). The post-enrichment

167   phase was excluded from the brown bear dataset, due to the start of hibernation. The locations the

168   enrichment was provided in varied throughout the experiment, to enhance the effect and keep the animals

169   interested in the enrichment (see Figure S1 for details of where the enrichment was placed). Observations

170   (enclosure use, behavioral patterns, activity budget, animal visibility and visitor flow) were performed

171   between 0800 AM and 0600 PM including the opening hours (1000 AM to 0400 PM) of the Wildlife

172   Park, in three time intervals: (1) 0800 AM till 1100 AM, (2) 1100 AM till 0200 PM, and (3) 0200 PM till

173   0600 PM. In total, we collected 95 observations for the brown bears (31 hours and 40 minutes, pre-

174   enrichment = 17 hours and 20 minutes, during enrichment = 12 hours and 20 minutes, post-enrichment =

175   2 hours; mean±SD observations per day = 3±2), 79 observations for the pine martens (26 hours and 20

176   minutes, pre-enrichment = 7 hours and 20 minutes, during enrichment = 9 hours and 40 minutes, post-

177   enrichment = 7 hours and 20 minutes; mean±SD observations per day = 2±1), 109 observations for the

178   domestic ferrets (36 hours and 20 minutes, pre-enrichment = 5 hours and 40 minutes, during enrichment =

179   6 hours and 20 minutes, post-enrichment = 6 hours and 40 minutes; mean±SD observations per day =

180   2±1), and 122 observations for the golden jackals (40 hours and 40 minutes, pre-enrichment = 17 hours

181   and 20 minutes, during enrichment = 10 hours and 20 minutes, post-enrichment = 13 hours; mean±SD

182   observations per day = 3±2). Observation lengths between phases varied, because observer availability

183   differed between phases. Observations were performed on group-level. To measure animal visibility (the

184   number of visible animals within the enclosure) and visitor flow (the number of people facing the

185   enclosures), observers stood at locations that were easily accessible for visitors. As the brown bear and

186   golden jackal enclosures were too big to get an overview of the whole area from one point alone, several

187   observation points were selected (three at the brown bears, two at the golden jackals). One observation

188   point was sufficient at the ferrets and pine martens.

189   **Enrichment**

190   The enrichment items provided to the different species were food-based (brown bear, pine marten,

191   ferret, and golden jackal) and olfactory enrichment (golden jackal). The time and location of enrichment

192   in the enclosure were determined after the 'pre-enrichment' phase, to adapt enrichment items to the needs

193   of each species (i.e. according to their enclosure space use and temporal behavioral pattern observed in

194   phase 1) and to enhance animal visibility for the visitors. The enrichment was introduced in the morning

195   between 0800 AM and 1100 AM, either additionally to the scheduled feeding (i.e. brown bears) or

196   outside the feeding context (i.e. golden jackal, pine marten, and ferret). During feeding, the brown bears

197   had to be confined in order to allow the animal caretakers to enter the enclosure and to distribute the food.

198   This had to be done for safety reasons, which was not the case with the other three species. To avoid

199   additional disturbances to the animals' temporal behavior patterns (additional confinements), we decided

200   to coordinate the enrichment procedure with the feeding schedule in the brown bear enclosure. The

201   enrichment was renewed every second day for the brown bears, pine martens, and ferrets, and once a

202   week for the golden jackals. Enrichment was removed from the enclosures the evening before the day of

203   renewal, to be renewed and placed in the enclosures the next morning. The timeline of the enrichment

204   renewal was chosen to facilitate coordination with the animal keepers and for logistic reasons. The timing

205   of enrichment (mainly regarding olfactory enrichment) presentation differed in golden jackals from that

206   of the other species because scent does not dissipate too quickly as long as a strong scent is used and to

207   avoid habituation of enrichment (Clark & King, 2008). Furthermore, as the golden jackals avoided the

208   presence of humans from the beginning, we tried to limit disturbance by entering the enclosure and

209   distributing food-based and olfactory enrichment to once a week. Observations were performed on all

210   days.

211   The brown bears received two 1 m long acacia logs as enrichment objects. Dried fruit, honey,

212   yogurt and nuts were hidden in drilled holes of various sizes, which could be obtained by intensive and

213   long-term activity. This references to bears in the wild spending about 50% of their active time with food

214   procurement (Seryodkin et al., 2013; Schneider et al., 2014). Food procurement consists largely of

215   collecting and consuming various small food items, in order to ultimately meet their energy needs. By

216   using the acacia logs, a natural behavior of food gathering is stimulated, that is often lost in zoo-housed

217   animals due to fixed feeding procedures and schedules (Grandia et al., 2001).

218   The pine martens and domestic ferrets were provided with an inter-crimped wire mesh (2x2 cm

219   holes) covered open-topped wooden box measuring approximately 20 cm x 20 cm. The holes in the wire

220   mesh were large enough for the animals to retrieve the food with their paws. The mesh was used to make

221   the enrichment more challenging and to keep the animals interested in the enrichment. The box was filled

222   with pine cones, bark, leaves, moss, cranberries, nuts, raisins, mealworms, and egg shells (egg shells were

223   only provided to the ferrets) that the animals could reach with their paws. Pine martens and domestic

224   ferrets can find this type of food in their natural environment, which they use to build up food stocks near

225   their dens, especially in autumn (i.e. the period of our data collection). The plant components can also be

226   found by both species in forest habitats (Marinis & Masseti, 1995; Bodey et al., 2011).

227   For the golden jackal we used both food-based and olfactory enrichment. As food-based

228   enrichment we provided hollowed out pumpkins filled with insects, such as mealworms and stick insects.

229   Golden jackals' diet in the wild is composed of small rodents, invertebrates, reptiles, birds, and plants

230   (mainly fruits; Giannatos, 2010; Markov & Lanszki, 2012). Studies have shown that golden jackals feed

231   on pumpkins (Brooks et al., 1993), making the combination of pumpkin and insects a good choice for

232   enrichment (Monika Fiby, personal communication). Olfactory enrichment was included to stimulate

233   enclosure exploration (Clark & King, 2008). We filled four jute bags (squares of about 50 cm x 50 cm)

234   with either Przewalski horse (*Equus przewalskii*), European wolf, or rat feces (all species are housed in

235   the Wildlife Park, the latter is used as food). The bags were randomly distributed in the enclosure and

236   were attached to trees with twine (always two bags on the ground and two bags 1 m above the ground).

237   **Measuring enclosure use and behavioral patterns**

238   All data were collected with the software Animal Observer ((Caillaud, 2016), Animal Observer

239   v1.0, https://fosseyfund.github.io/AOToolBox/). VP-S, SB, SF, IG, TH, and CJ performed the

240   observations. Observations were collected on all days within the different experimental phases. We used

241   instantaneous scan sampling (Altmann, 1974; Martin & Bateson, 2021). The animals were observed over

242   a time span of 20 minutes (randomized across species and the three time intervals), using four minutes

243   intervals as sample points. Depending on species- and enclosure-size, the enclosures were divided into

244   grids as follows: (1) 10 x 10 m grid for the brown bear enclosure, (2) 1 x 1 m grid for the domestic ferret

245   and pine marten enclosures, and (3) 5 x 5 m grid for the golden jackal enclosure. The squares of the grid

246   were labeled with letters and numbers. Enclosure use was recorded by marking the x,y position of each

247   individual at the end of each scan interval (i.e. every four minutes) on the enclosure map using the app.

248   Each x,y position was related to a square of the grid. Furthermore, behavioral data were collected as

249   binomial variables (i.e. behavior was observed/not observed during the scan): (1) behavior patterns, i.e.

250   self-maintenance and vigilance, locomotion (walking, pacing, climbing, hanging, approach/retreat),

251   affiliative and agonistic interactions between conspecifics and heterospecifics, object (enrichment and

252   other natural objects within the enclosure, such as stones, etc.) and human interaction and (2) activity

253   budget, i.e. activity in general (active, non-active). In addition, we recorded visibility (i.e. number of

254   animals visible at the moment of scan) and visitor flow at the moment of observation. Visitor flow was

255   defined as the number of people facing the enclosures (i.e. 0, <10, 10-20, >20 visitors at the enclosure)

256   during observations.

257   **Data analysis**

258   All analyses were performed using the software R 4.0.2 (R Core Team, 2020) and the package

259   'mgcv' (Wood, 2011). The 'post-enrichment' phase (data collected in November) was excluded from the

260   brown bear dataset, as both brown bears were already showing signs of starting hibernation and,

261   therefore, enclosure use and behavioral patterns were not comparable to the previous phases. Golden

262   jackals were excluded from the statistical analysis, as both individuals did not leave their burrows during

263   daytime during the entire observation period.

264   **Enclosure use.** The species' extent of enclosure use was assessed using the traditional Spread of

265   Participation Index (SPI, Dickens, 1955), as we were interested in the change that enrichment elicits in

266   enclosure use, rather than in the use of enclosure resources in general. The traditional SPI requires all

267   enclosure zones to be of equal size. The SPI was calculated for each combination of phase and time

268   interval (i.e. pre-enrichment 0800 AM – 1100 AM, pre-enrichment 1100 AM – 0200 PM, pre-enrichment

269   0200 PM – 0600 PM, enrichment 0800 AM – 1100 AM, enrichment 1100 AM – 0200 PM, enrichment

270   0200 PM – 0600 PM, post-enrichment 0800 AM – 1100 AM, post-enrichment 1100 AM – 0200 PM,

271   post-enrichment 0200 PM – 0600 PM). SPI values range from 0 (equal use of the enclosure) to 1 (unequal

272   use of the enclosure, i.e. some enclosure zone are preferred over others). The formula for the traditional

273   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

274   made across all enclosure zones, M is the mean number of observations made per enclosure zone, n_a is the

275   number of zones that have a total number of observations greater than M, n_b is the number of zones that

276   have a total number of observations fewer than M, F_a is the total number of observations in zones with

277   frequencies greater than M, and F_b is the total number of observations in zones with frequencies fewer

278   than M.

279   **Temporal behavioral patterns and activity budget.** To investigate whether enrichment

280   influences temporal behavior patterns (i.e. self-maintenance and vigilance, locomotion, affiliative and

281   agonistic interactions between conspecifics and heterospecifics, object and human interaction) and

282   activity budget (active, non-active) we used separate Generalized Linear Mixed Model (GLMM) with

283   binomial error structure and logit link function. We included phase, time interval, and visitor flow as

284   fixed factors. Originally, we included also the interaction between phase and time interval in all models.

285   However, some models did not converge, and therefore we excluded the interaction from the model.

286   Observation ID was added as random effect to account for the possibility that behavioral patterns varied

287   between scan samples. Each species and behavior were analyzed in separate models. Only observations

288   where the individual behaviors could be observed were used for the final sample size. The samples for the

289   brown bear models consisted of the following scan counts: 306 self-maintenance/other behavior scans (55

290   with self-maintenance), 306 locomotion/other behavior scans (46 with locomotion), 325 affiliative

291   interaction/other behavior (2 with affiliative interaction), 325 agonistic interaction/other behavior (1 with

292   agonistic interaction), 295 object interaction/other behavior scans (45 with object interaction), 325 human

293   interaction/other behavior (1 with human interaction), and 290 active/non-active scans (163 with activity).

294   The samples for the pine marten models consisted of the following scan counts: 959 self-

295   maintenance/other behavior scans (45 with self-maintenance), 959 locomotion/other behavior scans (321

296   with locomotion), 948 affiliative interaction/other behavior (14 with affiliative interaction), 948 agonistic

297   interaction/other behavior (68 with agonistic interaction), 948 object interaction/other behavior scans (71

298   with object interaction), 948 human interaction/other behavior (7 with human interaction), and 869

299   active/non-active scans (621 with activity).

300   The samples for the ferret models consisted of the following scan counts: 311 self-

301   maintenance/other behavior scans (19 with self-maintenance), 311 locomotion/other behavior scans (60

302   with locomotion), 289 affiliative interaction/other behavior (2 with affiliative interaction), 289 agonistic

303   interaction/other behavior (0 with agonistic interaction), 289 object interaction/other behavior scans (5

304   with object interaction), 289 human interaction/other behavior (5 with human interaction), and 155

305   active/non-active scans (125 with activity).

306   **Animal Visibility.** To analyze how the proportion of visible animals varied with phase, time

307   interval, and visitor flow (the number of people facing the enclosures) we used a GLMM with binomial

308   error structure and logit link function. Observation ID and scan sampling ID nested in observation ID

309   were included as random intercept. The reason for including this latter random intercept was that we had

310   multiple scans per observation. In R such an analysis of proportions is possible by using a two-columns

311   matrix with the number of visible and not visible individuals as the response.

312   Only observations where the individual behaviors could be observed were used for the final sample

313   size. The samples for the brown bear models consisted of the following scan counts: 450 visibility scans

314   (197 with visible animals).

315   The samples for the pine marten models consisted of the following scan counts: 468 visibility scans

316   (398 with visible animals).

317   The samples for the ferret models consisted of the following scan counts: 642 visibility scans (124

318   with visible animals).

319   As an overall test of the effect of the fixed effects we compared the full model with a null model

320   lacking the fixed effects but otherwise being identical to the full model using a likelihood ratio test.

321   To rule out collinearity we determined Variance Inflation Factors (VIF) for a standard linear model

322   excluding the random effect. No collinearity among phase, time interval and visitor flow was detected.

323   The models were fitted in R using the function glmer of the R package lme4. Tests of the individual

324   fixed effects were derived using likelihood ratio tests; R function drop1 with argument 'test' set to

325   'Chisq'.

326   **Results**

327   Regarding the golden jackals, both individuals did not leave their burrows during daytime during

328   the entire observation period. However, we know that the introduced enrichments were used during night,

329   which was recorded with wildlife cameras. For this reason, no observations of golden jackals were

330   possible, they were excluded from the statistical analysis.

331   **Enclosure use.** During enrichment, brown bears (Figure 1 B) used more zones of the enclosure in

332   the morning – in particular zones where enrichment was introduced – (SPI values: morning=0.686,

333   midday=0.881, afternoon=0.851), as compared to pre-enrichment (Figure 1 A, SPI values:

334   morning=0.955, midday=0.812, afternoon=0.806; Figure S2 A). In contrast, enrichment did not elicit a

335   change in enclosure use in pine martens (Figure 2, SPI values: pre-enrichment – morning=0.527,

336   midday=0.532, afternoon=0.444; enrichment – morning=0.518, midday=0.530, afternoon=0.496; post-

337   enrichment – morning=0.642, midday=0.560, afternoon=0.562; Figure S2 B) and domestic ferrets (Figure

338   3, SPI values: pre-enrichment – morning=0.567, midday=0.672, afternoon=0.612; enrichment –

339   morning=0.556, midday=0.537, afternoon=0.597; post-enrichment – morning=0.567, midday=0.505,

340   afternoon=0.672; Figure S2 C).

341   **Temporal behavioral patterns and activity budget.** Overall, there was a clear impact of the fixed

342   effects phase, time interval, and visitor flow on object interaction (likelihood ratio test comparing full and

343   null model: chi-squared=24.025, df=5, p<0.001) in brown bears. More specifically, object interaction in

344   brown bears was more frequently observed during the morning as compared to midday and afternoon

345   (marginal R^2 = 0.49; Table 1; Figure S3). However, phase and visitor flow had no effect on object

346   interaction. Phase, time interval, and visitor flow had no impact on activity (likelihood ratio test

347   comparing full and null model: chi-squared=10.579, df=5, p=0.060), locomotion (likelihood ratio test

348   comparing full and null model: chi-squared=1.971, df=5, p=0.853), and self-maintenance (likelihood ratio

349   test comparing full and null model: chi-squared=1.693, df=5, p=0.890) in brown bears.

350   In pine martens, there was an overall effect of the fixed effects phase, time interval, and visitor

351   flow on object interaction (likelihood ratio test comparing full and null model: chi-squared=19.524, df=6,

352   p=0.003), activity (likelihood ratio test comparing full and null model: chi-squared=16.549, df=6,

353   p=0.011), locomotion (likelihood ratio test comparing full and null model: chi-square=35.560, df=6,

354   p<0.001), and agonistic interaction (likelihood ratio test comparing full and null model: chi-

355   squared=25.307, df=6, p<0.001). Specifically, object interaction increased overall during enrichment and

356   was generally higher in the morning and during midday as compared to the afternoon (Figure S4). Pine

357   martens' activity (marginal $R^2 = 0.13$; Figure S5) and locomotion (marginal $R^2 = 0.14$; Figure S6)

358   increased from pre-enrichment to enrichment to post-enrichment. Furthermore, agonistic interactions

359   were observed less frequently during post-enrichment compared to the other phases (marginal $R^2 = 0.15$;

360   Figure S7), and fewer agonistic interactions occurred when fewer than 10 visitors were watching the

361   enclosure as compared to 0 and 10-20 visitors (Table 1). There was no obvious difference between time

362   intervals and visitor flow with regard to activity and locomotion, and agonistic interactions did not differ

363   between time intervals. The fixed factors phase, time interval, and visitor flow had no effect on self-

364   maintenance (likelihood ratio test comparing full and null model: chi-squared=2.689, df=6, p=0.847) in

365   pine martens.

366   Phase, time interval, and visitor flow had no impact on activity (likelihood ratio test comparing full

367   and null model: chi-squared=7.048, df=5, p=0.217), locomotion (likelihood ratio test comparing full and

368   null model: chi-squared=4.534, df=5, p=0.475), and self-maintenance (likelihood ratio test comparing full

369   and null model: chi-squared=9.809, df=5, p=0.081) in domestic ferrets.

370   Some behaviors were observed rarely (less than 5% of the total observations; e.g. affiliative and

371   human interactions for all three species, agonistic interactions for brown bears and domestic ferrets, and

372   object interactions for domestic ferrets) and where thus not included in the models.

373   **Visibility.** In brown bears, there was an overall effect of phase, time interval, and visitor flow on

374   the number of individuals visible at the moment of scan (likelihood ratio test comparing full and null

375   model: chi-squared=17.177, df=5, p=0.004; Figure S8). Visibility increased with the number of visitors

376   (marginal $R^2 = 0.09$; Table 2). Phase, time interval, and visitor flow had no obvious effect on the visibility

377   of domestic ferrets (likelihood ratio test comparing full and null model: chi-squared=8.323, df=5,

378   p=0.139) and pine martens (likelihood ratio test comparing full and null model: chi-squared=9.009, df=6,

379   p=0.173).

380

Discussion

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

383   support the assumption that enrichment elicits a change in enclosure use and behavioral patterns. First, as

384   expected, enrichment can increase enclosure use in brown bears. However, it had no effect on the use of

385   enclosure space in the other species, i.e. pine martens, domestic ferrets, and golden jackals. Second,

386   object interaction, activity in general, and locomotion increased in pine martens from pre-enrichment to

387   the enrichment phase and activity and locomotion remained high during post-enrichment. Third, visibility

388   in brown bears did not increase with enrichment, but rather with the number of visitors.

389   Enrichment resulted in a more homogeneous use of enclosure zones in brown bears – especially in

390   the zones where enrichment was introduced, while no effect was apparent in the other three species. The

391   change in enclosure use in brown bears as a result of enrichment is consistent with the findings described

392   for both brown bears and other species (brown bears, Soriano et al., 2015; kinkajous *Potos flavus,* Blount

393   & Taylor, 2000; fishing cats *Felis viverrina,* Shepherdson et al., 1993). Captive carnivores often show

394   low activity and enclosure use due to inadequate feeding conditions (Bashaw et al., 2003), which

395   encourages the inclusion of food-based or other types of enrichment. In the present study, a difference in

396   enclosure use was only apparent in the morning (0800 AM till 1100 AM) when the food-based

397   enrichment was freshly placed inside the enclosure. As the acacia logs filled with food were presented

398   only every second day in the morning, a prolonged and more frequent presentation of the enrichment, as

399   well as more frequent changes in location and selection of various hiding places, might enhance the effect

400   and maintain the desired change in a uniform use of different zones over time.

401   Unsuitable type or location and quantity of enrichment may affect the successful implementation of

402   enrichment (Weerd & Ison, 2019), which may have been the reason that domestic ferrets and pine

403   martens did not change their enclosure use. While the pine martens at least manipulated and inspected the

404   food-based enrichment, the domestic ferrets showed little interest in it. This suggests that the type of

405   enrichment was unsuitable for the domestic ferrets. Different objects that can be used for climbing or

406   digging boxes (e.g. boxes filled with rice in which small objects are hidden) could increase their interest.

407   The golden jackals in the current study responded to olfactory and food-based enrichment only during

408   night and were not visible at all during the observation period. Even though their wild counterparts show

409   higher activity patterns during night, diurnal movements occur on a smaller scale (Fenton et al., 2021).

410   However, the type of olfactory and food-based enrichment used may not have been the adequate type of

411   enrichment to change the activity patterns of this carnivorous species to diurnal rhythms. In particular, the

412   choice of scent seems to play an important role as not all scents achieve the desired goals and in some

413   cases can even decrease activity (Clark & King, 2008). We used semi-concentrated scents in jute bags,

414   which may have caused the scent to dissipate too quickly, causing the animals to lose interest. In this

415   respect to overall jackal findings, electronic feeders delivering food unpredictably in time rather than

416   conventional feeding seem to enhance activity (Kistler et al., 2009), suggesting that the unpredictability

417   and the need to search for food may be better suited to elicit a change in activity patterns in golden

418   jackals.

419   Enrichment can increase object interaction, activity in general, and locomotion in pine martens.

420   Enrichment with extrinsic reinforcement (such as food) seem to procure better and more prolonged

421   behavioral changes than ones with intrinsic reinforcements (i.e. behavior itself; Tarou & Bashaw, 2007).

422   The food-based enrichments used in the current study did not seem to be effective in the same way for all

423   study species. Only pine martens showed behavioural changes between phases. However, the timing of

424   food-based enrichment was rather predictable (i.e. the objects were always placed inside the enclosures at

425   approximately the same time), which may be a reason why the enrichment was not a success with all four

426   species. Activity rhythms are highly modifiable with food availability (Boulos & Terman, 1980; Ware et

427   al., 2012). The activity of pine martens in the wild, for instance, changes seasonally and tends to be

428   bimodal in autumn (Zalewski, 2001), which could have been a confounding factor for the changes found

429   for activity and locomotion. This would also explain why activity and locomotion remained high during

430   post-enrichment or even increased compared to the enrichment phase. Similarly, captive brown bears are

431   mainly diurnal with a strong crepuscular component (Ware et al., 2012) as compared to their wild

432   counterparts, which exhibit nocturnal behavior (Kaczensky et al., 2006). Therefore, the activity in this

433   study is consistent with the activity pattern of other captive bears, but diverges greatly from that of

434   animals living in the wild. Still, enrichment can contribute to improved welfare of the animals as it can

435   reduce stress of zoo-housed/captive animals (Hansen & Berthelsen, 2000; McDougall et al., 2006; Poessel

436   et al., 2011) and lack of species-typical inactivity would imply stereotypy (Renner & Lussier, 2002).

437   Furthermore, habituation can also influence the effectiveness of enrichment, which emphasizes that

438   enrichment should be slightly adapted each time of presentation to induce animals to use the enrichment

439   for longer periods (Tarou & Bashaw, 2007).

440   Contrary to expectations, enrichment did not enhance visibility of animals. But, for brown bears,

441   visibility increased with the number of visitors in front of the enclosure. This suggests that visitors can

442   also act as a form of enrichment for captive animals (Rault et al., 2020). Visitors can have positive

443   (Bloomfield et al., 2015; Hashmi & Sullivan, 2020), neutral (Sherwen et al., 2014) or negative (Davis et

444   al., 2005; Hashmi & Sullivan, 2020; Larsen et al., 2014) impacts on zoo-housed animals, depending on

445   the type of visual or acoustic interactions with the animals. For instance, meerkats (*Suricata suricatta*)

446   showed fewer social interactions during the zoo closure due to COVID-19 pandemic than during times

447   when visitors were allowed back into the zoos (Williams et al., 2021). However, this effect probably also

448   depends on the propensity of the animals to interact with humans, which may explain the discrepancy

449   found between species in the current study. Various bear species (e.g. sloth bears *Melursus ursinus*,

450   Andean bears *Tremarctos ornatus*, grizzly bears *Ursus arctos horribilis*, American black bears *Ursus*

451   *americanus*, Malayan sun bear *Helarctos malayanus*) seem to be more visible in the presence of visitors

452   (Bernstein-Kurtycz et al., 2021), while other species seem to show avoidance behavior (e.g. quokkas

453   *Setonix brachyurus*, Learmonth et al., 2018; orangutans *Pongo pygmaeus*, Birke, 2002; jaguars *Panthera*

454   *onca,* Sellinger & Ha, 2005). However, we have to be careful in interpreting the direction of these effects,

455   as visitors may be drawn to enclosures where animals are visible and active.

456   Although this study shows some findings that may suggest that food-based enrichment can, to some

457   extent, elicit a change in enclosure use and behavior in captive carnivore species, these results should be

458   interpreted with caution may not be generalizable to all other species and facilities due to the small

459   sample size and inconsistent results. Furthermore, the interpretation in this paper is constrained by the

460   limited time period and the changing season (e.g. start of hibernation in the brown bears). Thus, without

461   repeating the ABA design, it is not possible to attribute any changes to the manipulation. Other potential

462   problems are that (1) only one type of enrichment was used per species, (2) the observations were limited

463   to only one zoo, and (3) we did not find similar effects across species.

464   **Conclusion**

465   This study has shown that enrichment can elicit an increase in enclosure use for brown bears and an

466   increase in object interaction in pine martens. The results indicate the importance of evaluating long-term

467   effects of enrichment, as not all species reacted to the enrichment and no prolonged changes in enclosure

468   use or behavior were observed. Furthermore, before introducing enrichments, it is important to consider

469   whether the type of enrichment is suitable to achieve the desired goal and does not foster undesired

470   behavior. Thus, testing species-specific preferences of environmental enrichment prior to integrating and

471   presenting them in the enclosures, as well as testing their effect on enclosure use and behavior, is crucial.

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657

658 **Figure labels**

659 **Figure 1.** Brown bear enclosure use. The extent of enclosure use pre-enrichment (A) and during

660 enrichment (B) is shown on a scale (density level) from white (low) to red (high) for each square of the

661 10x10 m grid and divided into three time intervals. Density level indicates the total number of sightings

662 of individuals in a specific sector independent of activity level. Point size increases with activity level (i.e.

663 total number of sightings of active animals in a specific sector of the enclosure) per square. Enclosures

664 labelled with '1' is accessible for brown bears and European wolves. Enclosure labelled with '2' is only

665 accessible for the European wolves.

666 **Figure 2.** Pine marten enclosure use. The extent of enclosure utilization pre-enrichment (A), during

667 enrichment (B), and post-enrichment (C) is shown on a scale (density level) from white (low) to red

668 (high) for each square of the 10x10 m grid and divided into three time intervals. Density level indicates

669 the total number of sightings of individuals in a specific sector independent of activity level. Point size

670 increases with activity level (i.e. total number of sightings of active animals in a specific sector of the

671 enclosure) per square.

672 **Figure 3.** Domestic ferret enclosure use. The extent of enclosure utilization pre-enrichment (A), during

673 enrichment (B), and post-enrichment (C) is shown on a scale (density level) from white (low) to red

674 (high) for each square of the 10x10 m grid and divided into three time intervals. Density level indicates

675 the total number of sightings of individuals in a specific sector independent of activity level. Point size

676 increases with activity level (i.e. total number of sightings of active animals in a specific sector of the

677 enclosure) per square.

Table 1(on next page)

Results of the behavioral pattern models.

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 1. 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 CI	upper CI	χ^2	df	p	min	max
Brown bear object interaction									
intercept	-1.604	1.037	-18.214	0.572			[1]	-2.534	-0.341
phase (during enrichment)[2]	0.955	1.021	-1.235	17.535	0.827	1	0.363	-0.241	1.911
time interval (1100 AM – 0200 PM)[3]	-2.424	1.065	-64.351	-0.900	15.069	2	0.001	-3.128	-1.838
time interval (0200 PM – 0600 PM)[3]	-3.655	1.206	-74.415	-2.017				-22.912	-3.389
visitor flow (<10)[4]	-0.808	0.878	-13.350	0.904	1.569	2	0.456	-1.245	-0.314
visitor flow (10-20)[4]	0.516	0.759	-1.196	2.127				0.085	0.866
Pine marten activity									
intercept	0.677	0.494	-0.275	1.686			[1]	0.488	0.949
phase (during enrichment)[2]	1.632	0.516	0.713	2.660	12.455	2	0.002	1.460	1.787
phase (post-enrichment)[2]	1.694	0.557	0.572	2.788				1.518	1.835
time interval (1100 AM – 0200 PM)[3]	-0.801	0.453	-1.708	0.052	4.104	2	0.128	-1.319	-0.706

time interval (0200 PM – 0600 PM)[3]	-0.010	0.537	-1.027	1.089				-0.290	0.162
visitor flow (<10)[4]	-0.165	0.230	-0.627	0.288	0.568	2	0.753	-0.266	-0.046
visitor flow (10-20)[4]	0.190	1.014	-1.665	12.760				-1.277	1.295
Pine marten locomotion									
intercept	-1.272	0.318	-1.910	-0.670			[1]	-1.389	-1.112
phase (during enrichment)[2]	0.185	0.306	-0.418	0.762	32.104	2	<0.001	0.026	0.296
phase (post-enrichment)[2]	1.805	0.336	1.204	2.492				1.708	1.909
time interval (1100 AM – 0200 PM)[3]	-0.070	0.296	-0.632	0.562	2.837	2	0.242	-0.193	-0.003
time interval (0200 PM – 0600 PM)[3]	0.402	0.316	-0.212	1.034				0.296	0.475
visitor flow (<10)[4]	-0.116	0.197	-0.529	0.263	0.835	2	0.659	-0.184	-0.033
visitor flow (10-20)[4]	-0.581	0.799	-2.615	0.999				-14.256	-0.017
Pine marten agonistic interaction									
intercept	-2.255	0.563	-3.489	-1.320			[1]	-2.587	-2.110
phase (during enrichment)[2]	0.414	0.539	-0.668	1.515	8.871	2	0.012	0.254	0.670

phase (post-enrichment)[2]	-1.401	0.674	-3.154	-0.093				-1.755	-1.108
time interval (1100 AM – 0200 PM)[3]	-0.760	0.525	-1.857	0.303	2.131	2	0.345	-0.933	-0.567
time interval (0200 PM – 0600 PM)[3]	-0.478	0.557	-1.689	0.687				-0.733	-0.262
visitor flow (<10)[4]	-1.485	0.422	-2.597	-0.739	17.061	2	<0.001	-2.291	-1.220
visitor flow (10-20)[4]	1.063	0.986	-19.019	3.079				-13.784	2.968
Pine marten object interaction									
intercept	-4.923	0.989	-18.442	-3.325			[1]	-5.451	-4.632
phase (during enrichment)[2]	3.539	0.903	1.958	16.923	17.164	2	<0.001	3.306	4.128
phase (post-enrichment)[2]	0.300	1.180	-14.051	13.874				-0.479	0.997
time interval (1100 AM – 0200 PM)[3]	-1.382	0.788	-3.085	0.217	4.764	2	0.092	-1.702	-1.173
time interval (0200 PM – 0600 PM)[3]	-1.918	0.878	-4.097	-0.206				-2.423	-1.706
visitor flow (<10)[4]	0.271	0.418	-0.550	1.121	0.632	2	0.729	0.107	0.400
visitor flow (10-	-12.903	323.817	-16.060	-8.563				-14.419	-

20)[4]									11.960

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

8

Table 2(on next page)

Results of the visibility model.

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 2. 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 CI	upper CI	χ^2	df	p	min	max
Brown bear visibility									
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

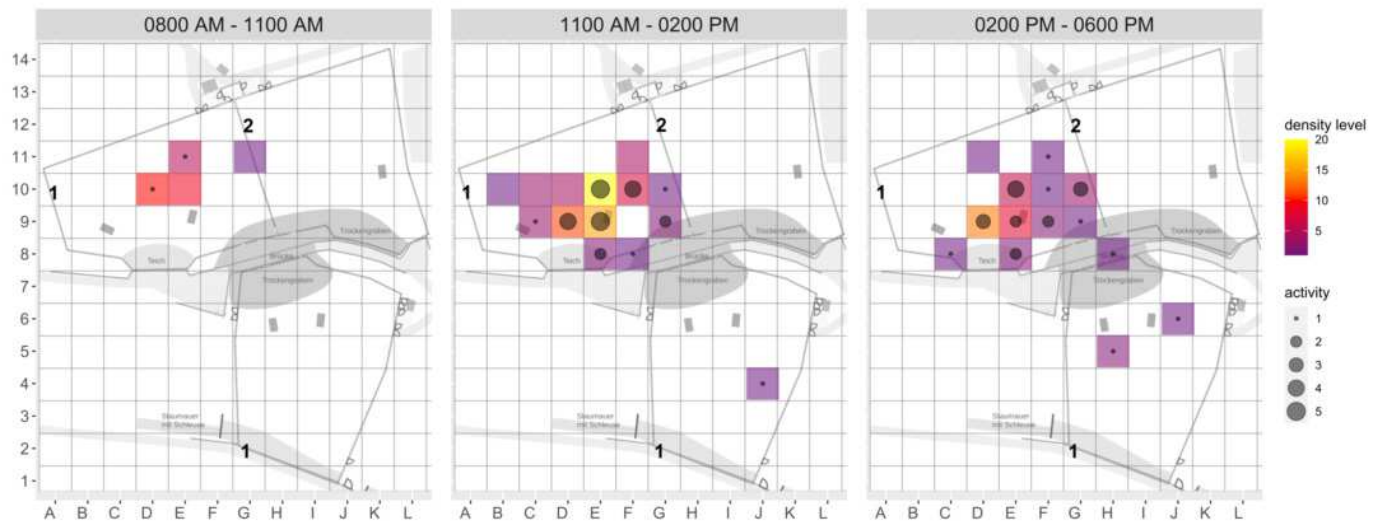7   [4]dummy coded with 0 visitors being the reference category

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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. Density level 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.

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. Density level 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.
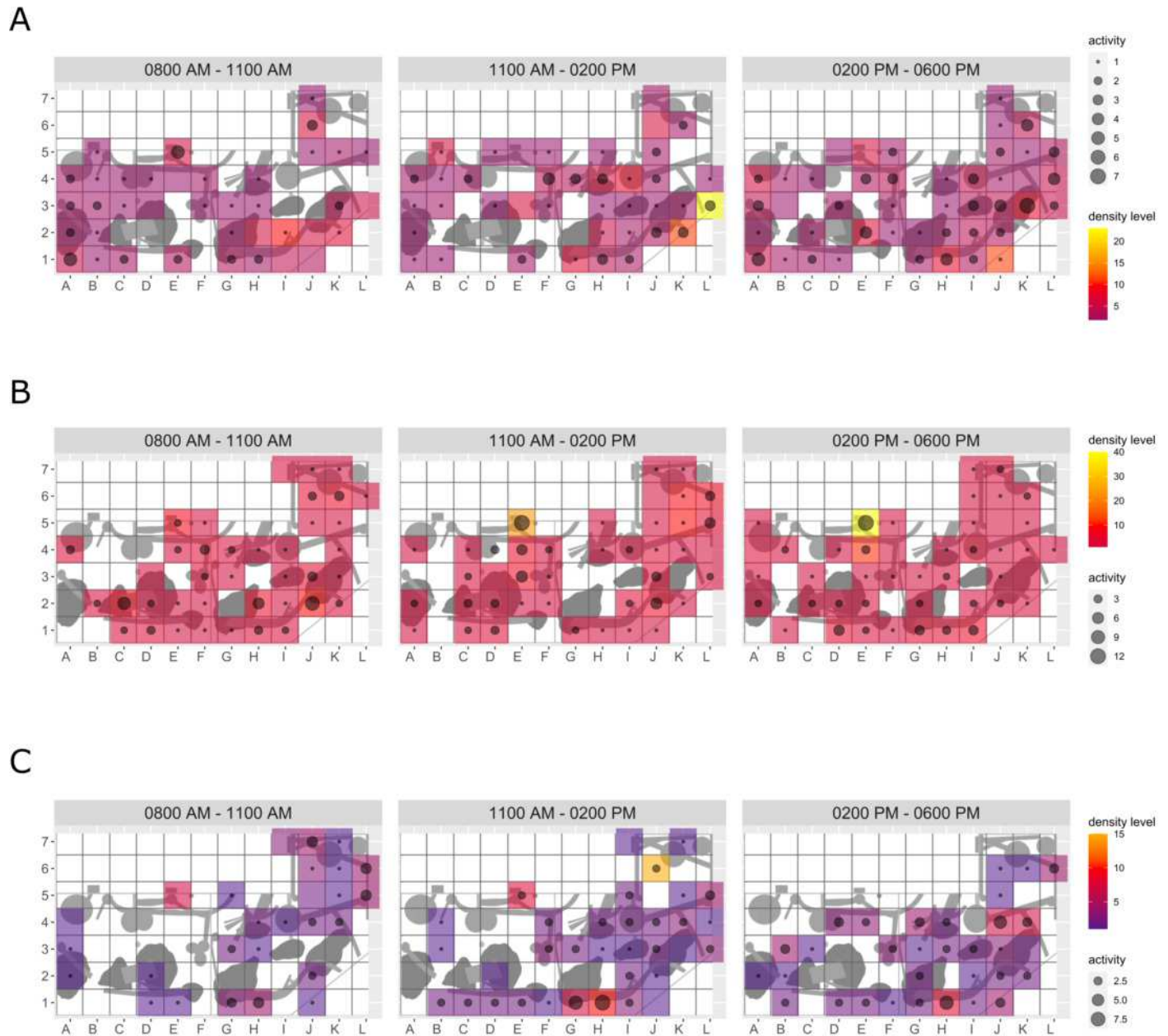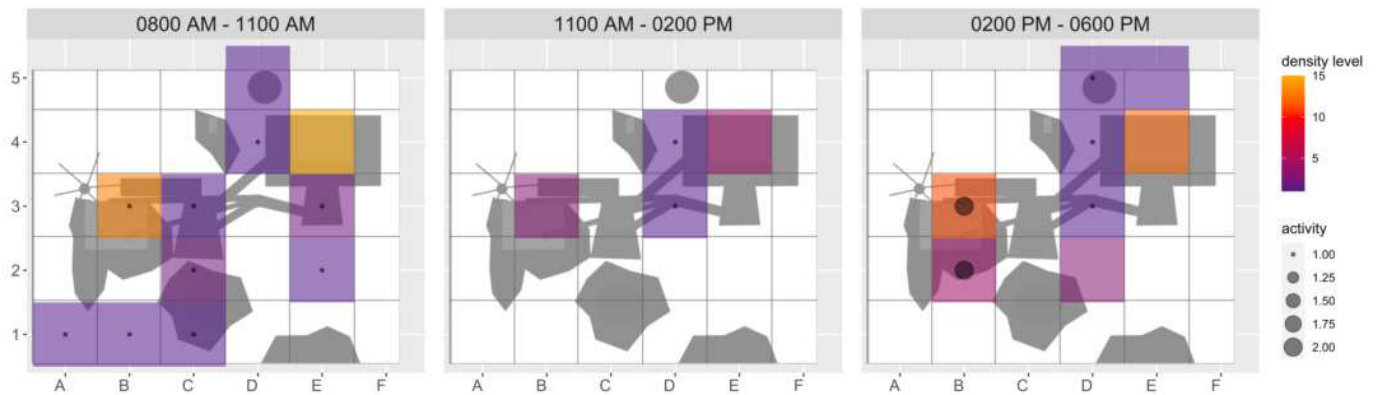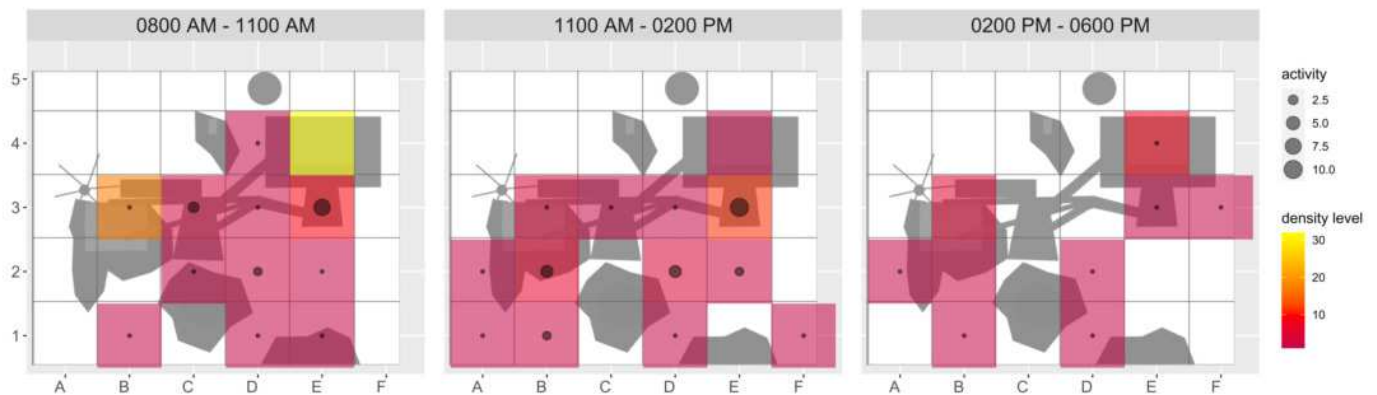
A

B

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. Density level 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.