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Structural enrichment and enclosure use in an opportunistic carnivore: the red fox (Vulpes vulpes)

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Abstract

*An increasing number of zoos keep their animals in natural-looking enclosures, but it is often unclear whether or not the species' behavioural and ecological needs are being adequately met. For species that suffer predation in the wild, structural enrichment in captivity can play a crucial role in connection with enclosure use. Firstly, we examined the effectiveness of structural enrichment in modifying enclosure use in an opportunistic carnivore, the red fox (*Vulpes vulpes*). In a test enclosure, we placed both long wooden and cover structures that simulated natural habitat in predetermined sectors. A group of four foxes were exposed to four treatments: (i) structural enrichment in location 1 (LOC1s); (ii) structural enrichment in location 2 (LOC2); (iii) structural enrichment removed (REM); and (iv) structural enrichment again in location 1 (LOC1e). Sectors containing long wooden structures were preferred significantly compared to the rest of the enclosure. Sector use was selectively shifted to those in which cover structures were present. Structural enrichment had no significant effect on activity. Secondly, in a new outdoor enclosure, we compared the use of sectors with cover or elongated structures with that of corresponding sectors without structures. All individuals showed a significant preference for sectors containing structures. In the course of the three-week observation period, there was a significant decline in preference for structures and a significant increase in activity (week 1 < week 2 = week 3). These results suggest that in medium-sized carnivores, structural enrichment is beneficial when natural features with a net-like distribution over the habitat are simulated.*

Keywords: *animal welfare, environmental enrichment, red fox, structural preference,* Vulpes vulpes*, zoo*

Introduction

Structural enrichment can enhance the complexity of captive environments (Maple & Perkins 1996), but in contrast to feeding enrichment, structural enrichment is rarely applied in zoos (Schetini de Azevedo *et al* 2007). Nevertheless, an increasing number of zoo exhibits are designed to mimic animals' natural habitat (Robinson 1998). Outdoor enclosures offer spatial variation due to natural elements dividing the enclosure into various sections, and temporal variation due to daily and seasonal changes (Hutchins *et al* 1984). Richly structured enclosures provide animals with a variety of stimuli and structure space both horizontally and vertically (Hediger 1942; Maple & Perkins 1996). It is often thought that environmental complexity is highest in natural-looking enclosures thereby allowing the animals to display their natural behaviour (Hutchins *et al* 1984). However, even in natural-looking enclosures, the placement of structures needs to be well considered and adjusted to the animals' use of structures (Hutchins *et al* 1984). Moreover, functional substitution of natural elements with structures that serve the same function has been applied successfully in the past (Mellen *et al* 1981; Markowitz 1982; Robinson 1998). Various carnivore species kept in captivity are highly exploratory, and activities including foraging, territorial, social and play behaviour can cover a considerable part of the animal's daily time budget (Poole 1992). Enclosures need therefore to be furnished such that animals' ecological and behavioural needs are met, thereby guaranteeing their well-being (Hughes & Duncan 1988; Broom 2007).

Previous studies have shown that structural enrichment reduces abnormal behaviour or elicits natural behaviour. In spectacled bears (*Tremarctos ornatus*) pacing and sitting motionlessly were reduced and general activity increased by the addition of climbing structures (Renner & Lussier 2002). In a study on clouded leopards (*Neofelis nebulosa*), tight ropes elicited natural climbing behaviour (Hartmann & Schiess 1997), and Indian leopards (*Panthera pardus*) performed less stereotypic behaviour when the outdoor enclosure was furnished with natural features (Mallapur &

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Chellam 2002). In captivity, cover is an important feature for species that suffer a high risk of predation and whose natural habitats are rich in cover. Thus, adding cover structures to the cages reduced stereotypic behaviour in bank voles (*Clethrionomys glareolus*), gerbils (*Meriones unguiculatus*) and laboratory mice (Ödberg 1987; Wiedenmayer 1997; Würbel *et al* 1998). Japanese quail (*Coturnix japonica*) showed less flight responses to a flight-inducing stimulus when cages were enriched with cover structures (Buchwalder & Wechsler 1997). Stereotypic running in fennec fox (*Fennecus zerda*) was elicited through noise from keepers and visitors. The lack of space and hiding places was regarded as the main cause for this abnormal behaviour (Carlstead 1991). Gusset (2005) hypothesised that hiding as a coping strategy can reduce stress in margays (*Leopardus wiedii*) showing stereotypic behaviour. In farmed foxes (*Vulpes vulpes, Alopex lagopus*), abnormal behaviour was attributed to the barren cages and fear of humans (Nimon & Broom 2001). Red foxes (*V vulpes*) have evolved in an environment in which they suffered predation from larger canid or felid species as well as humans. Their habitat includes cover-rich areas, and fox trails are frequently found along natural structures (Lucherini *et al* 1995; Adkins & Stott 1998; White *et al* 2006). Therefore, captive foxes may benefit from structural enrichment that takes into account the environment within which they have evolved and become adapted to.

In the first part of this study, two experiments on structural enrichment were conducted with a group of four foxes housed in a near-to-natural outdoor enclosure. We used two types of enrichment, long wooden structures and cover structures. Long wooden structures were designed as substitutes for hedges or walls and provided foxes the possibility to move along a structure while ranging in the enclosure. Cover structures were designed as substitutes for scrub or thicket through which the foxes could slip while ranging in the enclosure. The experimental structures were placed in predetermined sectors, shifted in location, and removed from the enclosure. We tested the efficiency of these structural enrichments in influencing enclosure use and enhancing activity. Our prediction was that the foxes' preference for sectors would shift depending on the location of the structural enrichment. Furthermore, we expected the activity to be higher in treatments with structural enrichment than in those without. Thus, the aim of the first part of the study was to assess preferences for structural components in a species that lives in cover-rich habitats.

In the second part of this study, we conducted an experiment on structure use in a newly built, natural-looking enclosure into which the same group of foxes were transferred. Various structures were placed in the enclosure to provide cover. We tested the foxes' preferences among eleven of these structures in comparison to virtual structures that were assigned to each of the eleven real structures. We expected foxes to prefer the real structures over the virtual structures. We also expected activity to increase in the course of the observation period. The aim of the second part of the study therefore was to test whether the structures in the new enclosure were used by the foxes, thereby serving their purpose.

Materials and methods

Experiment I — Experiments in test enclosure

Subjects and housing

This study was conducted in an outdoor enclosure at Langenberg Wildlife Park near Zürich, Switzerland. The enclosure was not accessible to visitors, but designed as a test case for a new exhibit to be planned for foxes in the public part of the park. We refer to it therefore as the test enclosure.

The study subjects consisted of a group of four unrelated adult red foxes; two males and two females. All had been found as cubs in 2002 and thereafter lived together in the test enclosure. None of the females reared cubs during the study period. The outdoor enclosure spanned an area of 300 m^2 of natural soil covered with grass and other plants. It was furnished with various structures, such as a variety of resting places, shrubs, hedges composed of small fir trees, trees suitable for climbing, heaps of stones and earth, a wooden den and two artificial dens. Human intervention at the den never occurred during observation periods in order to provide the animals with a secure place of retreat.

Behavioural observations and structural enrichment experiments were carried out from July 2004 to October 2004, when foxes were two years of age. The daily food intake consisted of 400 g of meat and 200 g of fruit, nuts and raisins, with food provided by electronic feeders (Hartmann-Furter 2000), a self-service food box and manual scattering and hiding of food to simulate the situation in the wild. For a detailed description of this temporally and spatially unpredictable feeding method that stimulated natural foraging behaviour, see Kistler *et al* (2009).

Structural enrichment with wooden structures

The foxes were presented with four consecutive treatments. At the start, in treatment one (wLOC 1s), four long wooden structures were placed at four different sites in the enclosure. These structures had to be placed at the flat part of the enclosure (Figure 1, top). The structures consisted of four wooden walls: two that measured 600 × 2 × 80 cm (length × breadth × height) and two that were 600 × 50 × 80 cm. In treatment two (wLOC 2), each of the four long wooden structures were moved from the initial sites to new sites. The distance to the first location was approximately five meters. In treatment three (wREM), the four long wooden structures were removed from the enclosure and in treatment four (wLOC 1e), the four long wooden structures were replaced at the same location as in wLOC 1s.

Structural enrichment with cover structures

After the experiment with the long wooden structures, the foxes were presented with four different treatments concerning use of cover (Figure 1, middle).

In treatment one (cLOC 1s), nine wooden cover structures were placed at nine different sites in the enclosure (Figure 1, middle). Cover structures were 80 × 50 cm (length × breadth). Six were artificial solid wooden passages, and three were hollow stumps through which the foxes could slip. Of the three hollow stumps only two were

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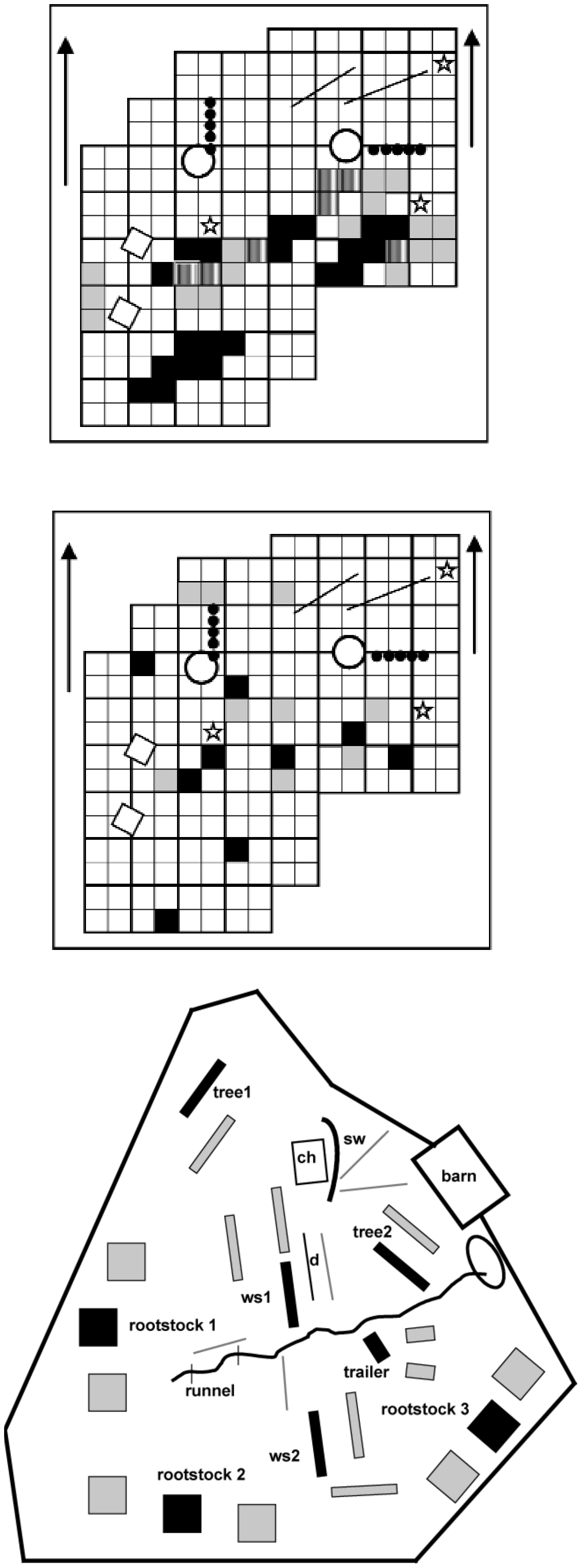
Figure 1



Test enclosure and quadratic sectors during experiments with long wooden structures (top) and cover structures (middle). Black squares: sectors containing experimental structures in treatments 1 and 4 (LOC 1s and LOC 1e), grey squares: sectors containing experimental structures in treatment 2 (LOC2), vertically lined squares: sectors that contained experimental structures in treatments 1, 2 and 4, white sectors: rest of enclosure (R), open circles: artificial dens, open rectangles: doghouse and wooden den, black circles: hedges, black lines: felled trees, stars: electronic feeders. The black arrows indicate the slope in the enclosure. New enclosure (bottom) with 11 real (black) and corresponding virtual (grey) structures, ch: chicken house, d: declivity, sw: stone wall, ws1 and ws2: wooden stacks.

available to the foxes at any given time, and one was blocked with wooden planks. In total, eight cover structures were accessible to the foxes.

In treatment two (cLOC 2), each of the six wooden passages and one hollow stump were moved to a new site. The distance to the first location was approximately five meters. The hollow stump that was blocked in treatment one was now opened and the other one blocked with wooden planks.

In treatment three (cREM), the six wooden passages were removed from the enclosure and all hollow stumps were blocked with wooden planks.

In treatment four (cLOC 1e), the six wooden passages and one hollow stump were placed in the same locations as LOC 1s, and the same hollow stump, which had been accessible in treatment one, was re-opened.

Experimental set-up and data recording

To record the pattern of structure use, the enclosure was divided into 211 sectors, each measuring 1.25 × 1.25 m. In the experiment on long wooden structures, 20 sectors contained experimental structures in treatments one and four, and 16 contained experimental structures in treatment two. In the experiment on cover structures, nine sectors contained experimental structures in treatments one, two, and four. Sectors containing no experimental structures were referred to as the rest of the enclosure. Each of the four treatments in both manipulations lasted for a period of one week. After three days of habituation to the structural enrichment, behavioural data were collected on days four, five and seven for five hours a day between 1200 and 2030h. After the last observation bout on day seven, experimental structures were manipulated according to the experimental set-up. Behavioural data were collected by direct observations from an elevated hide with the aid of binoculars. The foxes were accustomed to the observer's presence on the hide. For definitions of behaviours recorded, see Kistler *et al* (2009).

Activity of the individuals and use of structures were recorded using scan sampling at 2.5-min intervals (Altmann 1974). Activity was defined as all behaviours except resting and sleeping.

Data analysis

To assess use of sectors in the four treatments, the number used was summed over total observation time per treatment and individual (15 h), and the ratio s1/s2 calculated where s1 refers to sectors that contained experimental structures in treatments one and four, respectively, and s2 sectors that contained experimental structures in treatment two. To assess the preference for sectors containing experimental structures over the rest of the enclosure (R), the ratio (s1 + s2)/R was calculated per treatment and per individual.

To determine activity, the number of active behaviours was summed over total observation time per treatment and per individual, and the proportion of active behaviour was calculated.

A Friedman test (Zar 1999) was used to test for significant differences in individual behaviour between the four treatments for all parameters. In the case of overall significance ($P \leq 0.05$), *post hoc* tests, after Conover (1980), were used to compare single treatments. SPSS (Version 13.0 for Windows) was used for all statistical tests.

Experiment 2 — Structure use in large new enclosure

Subjects and housing

In September 2007, all four individuals were transferred to a newly built enclosure in the Langenberg Wildlife Park. The natural-looking enclosure spanned 4,000 m^2 and had been designed as an agricultural landscape. It was richly furnished with elements that can be found on a farm, such as a chicken house, a trailer, an orchard, a runnel (that ran vertically through the centre of the enclosure from the upper to the lower side), wooden stacks, rootstocks, felled trees, and various shrubs. There were two artificial dens. The structures were arranged, netlike, such that they offered cover at various points when the foxes ranged in the enclosure. Visitors had access to the enclosure only on its lowest side where they could also enter a barn. The barn had open windows on the side that faced the enclosure offering a view over the whole enclosure. As electronic feeders were not yet operational during the study period, food was scattered manually and hidden by the observer before observations started throughout the entire enclosure except in the experimental areas designed to test the use of real or virtual structures. Food consisted of meat or rats, fruit, nuts, dried dog food, sunflower seeds and raisins.

Experimental set-up and data recording

The following eleven structures were used during behavioural observations besides the chicken house, six fruit trees, and newly planted bushes: two wooden stacks (6 × 2–3 m; length × height), two tree trunks of 8 m length and 1–2 m diameter, a stone wall of 12 × 1.5 m (length × height), a section of the declivity of 8 m length, including the second artificial den, a section of the runnel of 5 m length, the trailer of 6 × 2 × 1 m (length × breadth × height) and three big rootstocks with a diameter of 4 m and height of 2 m (Figure 1, bottom). To each of these structures, two virtual structures of similar size were assigned in a distance of approximately 4 m to the real structure. The edges of these virtual structures were marked with sticks resulting in a corresponding area containing no structures, only grass. Due to space restrictions, only one virtual structure was assigned to each of the two felled trees and the declivity.

Data recording took place for three weeks starting one day after the transfer of the foxes. Data were collected for three days a week and four hours a day between 1300 and 1830h. Behavioural data were collected by direct observations with the aid of binoculars from the visitor's barn from where the entire enclosure could be overlooked. During data collection, public access to the enclosure was not permitted. The same ethogram was used as for the experiments in the test enclosure. To record activity and use of real and virtual structures, scan sampling at 2.5-min intervals (Altmann 1974) was used.

Data analysis

In order to obtain a preference value for structure use, the Jacobs' preference index (Jacobs 1974) was calculated as:

$J = (r–P)/([r+P]–2rP)$

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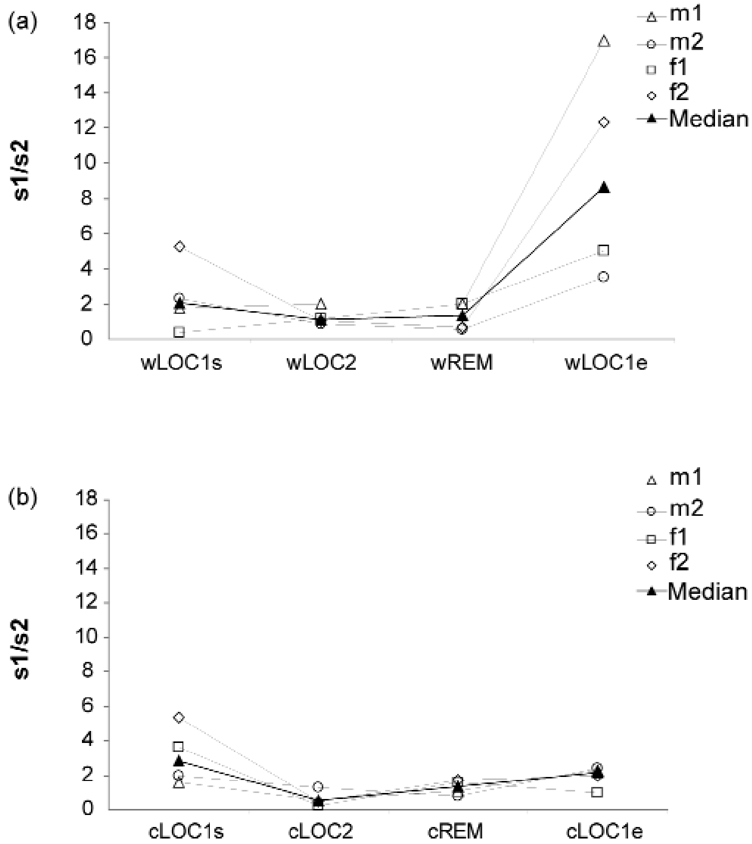
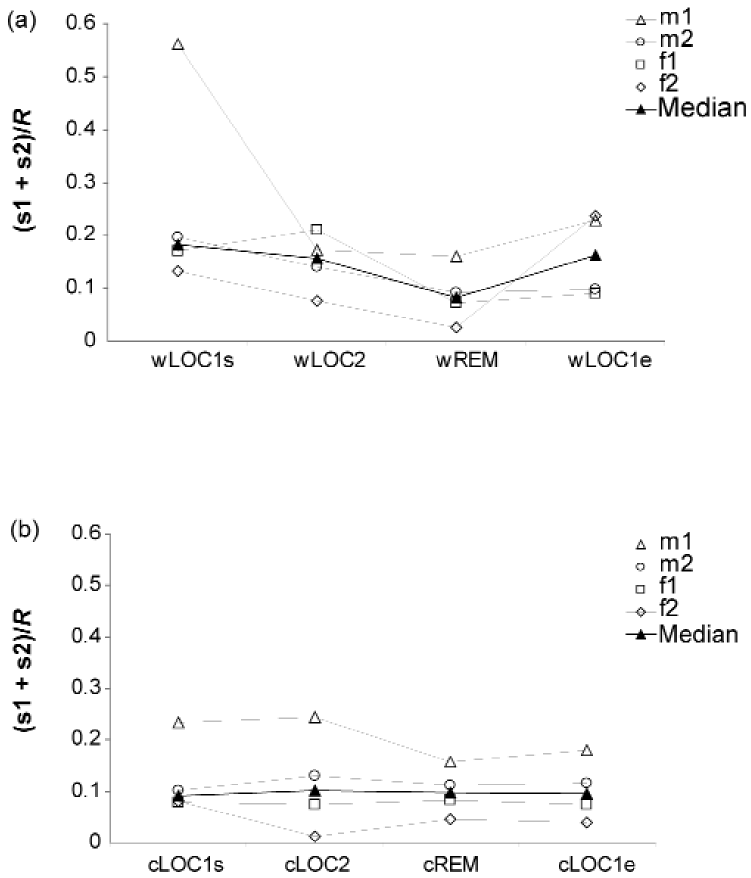
Figure 2



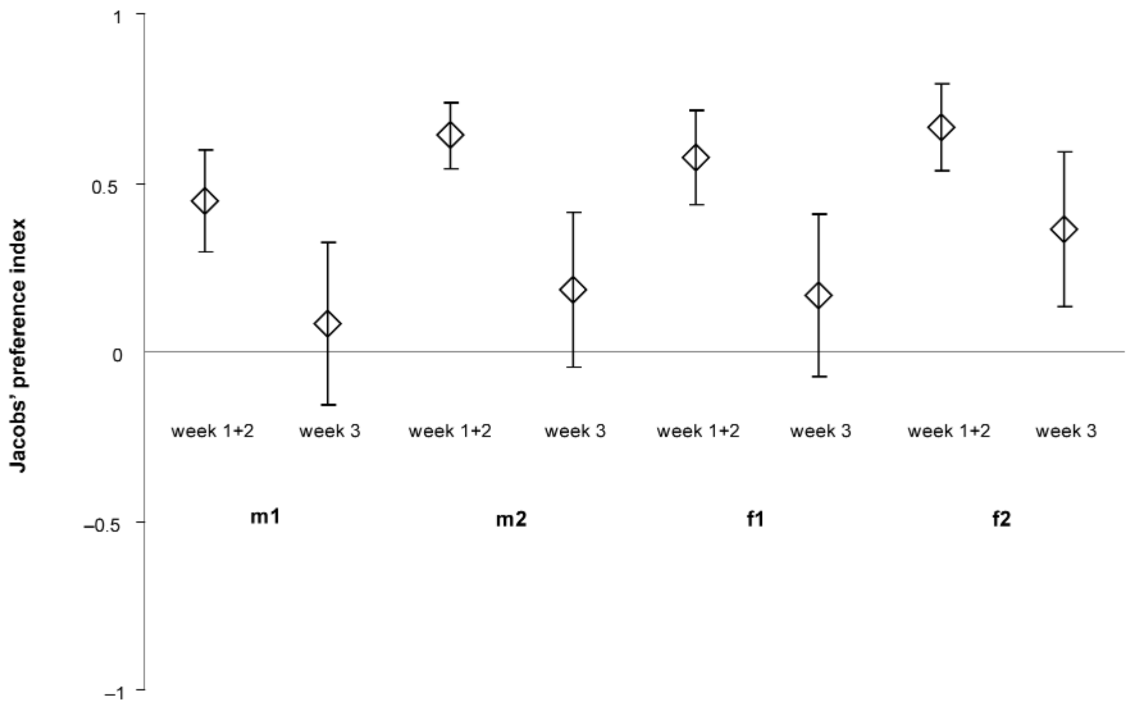
Individual use of experimental structures by four red foxes (two males, m1, m2, and two females, f1, f2) during four treatments (LOC 1s, LOC 2, REM, LOC 1e; for abbreviations of treatments see *Materials and methods*), after enrichment with either (a) long wooden structures or (b) cover structures. Ratios and overall medians are shown for s1/s2 (s1: sectors of the test enclosure containing structures during LOC 1s and LOC 1e; s2: sectors containing structures during LOC 2).

Figure 3



Individual preferences of sectors with experimental structures during four treatments (LOC 1s, LOC 2, REM, LOC 1e, after enrichment with either (a) long wooden structures or (b) cover structures. Ratios and overall medians are shown for (s1 + s2)/*R* (s1: sectors of the test enclosure containing structures during LOC 1s and LOC 1e; s2: sectors containing structures during LOC 2; *R*: rest of enclosure).

Figure 4



Jacobs' preference indices (see *Materials and methods* for description) for the use of eleven areas with structures over comparably sized areas without structures in a large, natural-looking enclosure by four red foxes (two males, m1 and m2, and two females, f1 and f2). Positive values indicate preference, negative values avoidance. Individual means (± SEM) for the period week 1+2 and week 3.

where *r* is the ratio of the number of real structures used to the number of all real and virtual structures used, and *P* is the available proportion of each structure. Thus, for structures with two virtual structures ($P = 0.333$), and for structures with one virtual structure ($P = 0.5$). The index ranges between +1 for maximum preference, and –1 for maximum avoidance. To examine preference for real structures over the whole observation period (36 h), the index was calculated per individual and per structure. To test for non-random use of structures (significant difference from zero) a one-sample *t*-test was conducted (with n–1 degrees of freedom, where n is the number of structures used in the analysis).

To examine development in structure use over time, we calculated the Jacobs' preference index for all structures per individual separately for the first two weeks and the third week. Fox activity was rather low during the first week, therefore data for the first and second week were pooled. For comparison of the two periods, a Wilcoxon signed ranks test was used (Zar 1999).

To measure activity, the number of active behaviours was totalled per week and per individual, and the mean proportion of active behaviour was calculated. A Friedman test (Zar 1999) was used to test for significant differences in individual activity between the three weeks. In the case of overall significance ($P \leq 0.05$), *post hoc* tests after Conover (1980) were used to compare single treatments. SPSS (Version 13.0 for Windows) was used for statistical tests.

Results

Effects of structural enrichment on spatial behaviour in the test enclosure

The foxes increased the use of the long wooden structures during treatment four (wLOC 1e), when the structures were replaced after having been removed, although this increase only reached the level of a non-significant trend (c2 = 7.462, df = 3, n = 4, $P = 0.053$; Figure 2a). When the long wooden structures were present, however, the foxes showed significantly greater preference for these enriched sectors compared to the rest of the enclosure (c2 = 8.1, df = 3, n = 4, $P = 0.036$; Figure 3a). The lowest median preference ratio occurred when the structures were removed from the enclosure (wREM; *post hoc* comparisons wREM < wLOC 1s = wLOC 2 = wLOC 1e, all $P < 0.05$).

The use of sectors with cover structures differed significantly between treatments (c2 = 8.1, df = 3, n = 4, $P = 0.036$; Figure 2b), with the peak median ratio in the first treatment (cLOC 1s) and lowest median ratio when structures were dislocated (cLOC 2; *post hoc* comparisons cLOC 1s = cLOC 1e > cLOC 2 = cREM, all $P < 0.05$). The foxes did not differ significantly in their preferences for sectors with cover structures and after removal of such enrichment in comparison to the rest of the enclosure (c2 = 0.538, df = 3, n = 4, $P = 0.946$; Figure 3b).

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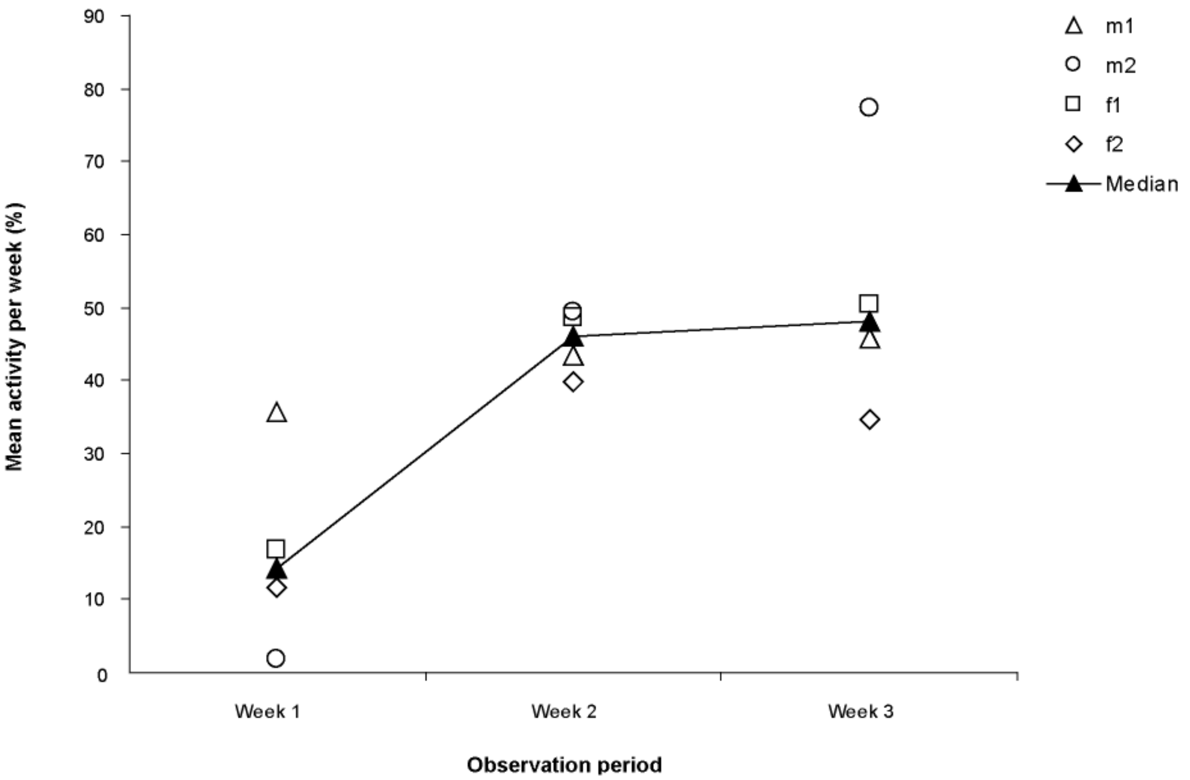
Figure 5



Percentage of activity (individual weekly mean and overall median) of four red foxes (two males, m1 and m2, and two females, f1 and f2) after transfer into a large natural-looking enclosure over a three-week study period.

Effects of structural enrichment on activity in the test enclosure

In the experiment with the long wooden structures, overall fox activity did not differ significantly between the four treatments (median activity [± SEM]: wLOC 1s: 42.5 [± 0.68]%, wLOC 2: 38.6 [± 0.58]%, wREM: 42.3 [± 0.53]%, wLOC 1e: 49.2 [± 0.75]%; c2 = 8.1, df = 3, n = 4, $P = 0.68$).

In the experiment with cover structures, overall activity differed significantly between treatments (c2 = 8.4, df = 3, n = 4, $P = 0.018$), with similar median activity in treatments one (cLOC 1s: 55.2 [± 0.52]%) and two (cLOC 2: 56.4 [± 0.61]%) and decreasing median activity in treatment three (cREM: 52.1 [± 0.60]%) and four (cLOC 1e: 43.5 [± 0.33]%). *Post hoc* comparisons revealed that the foxes were least active in the treatment when the cover structures were placed back at location one after having been removed from the enclosure (cLOC 1e < cLOC 1s = cLOC 2 = cREM, all $P < 0.05$).

Use of structures in the large new enclosure

All four study individuals showed a significant overall preference for the eleven structures over comparable areas not providing structures in the large enclosure (Jacobs' preference indices: m1: $t = 4.280$, df = 10, $P = 0.002$; m2: $t = 3.812$, df = 10, $P = 0.003$; f1: $t = 4.658$, df = 10, $P = 0.001$; f2: $t = 4.313$, df = 10, $P = 0.002$). Such preferences were significantly higher during the first two weeks compared to the third week ($Z = -2.578$, $P = 0.007$, n = 11; Figure 4).

Activity in the new enclosure

Overall activity of the four foxes increased significantly over the three-week observation period (c2 = 6.5, df = 2, n = 4, $P = 0.042$). *Post hoc* comparisons revealed a significant difference in activity between weeks 1 and 2, and between weeks 1 and 3 (week 1 < week 2 = week 3, $P < 0.05$; Figure 5).

Discussion

Influence of experimental structures on behaviour

Introducing structural elements in the test enclosure affected the spatial behaviour of a group of two male and two female red foxes. The different features of the long wooden structures and the cover structures, respectively, had different effects on the foxes' spatial behaviour. The four subjects may have influenced each other in their behaviour. In family groups of red foxes, interactions between all members occur, although with different frequencies depending on dominant or subordinate status (Baker & Harris 2000). However, foxes range alone in their territory though they might follow the same routes (Macdonald 1988; Doncaster & Macdonald 1997), and are solitary foragers which do not share food with conspecifics (Contesse *et al* 2004; Kistler *et al* 2009). Therefore, we treated the four individuals as statistically independent units with respect to the outcome measures taken.

The foxes generally preferred sectors containing long wooden structures over the rest of the enclosure, but showed only a non-significant tendency to preferentially use the relocated long wooden structures. The long wooden structures were concentrated in the flat part of the enclosure. If the foxes ranged in this region, they preferred to use these long structures to move along. Thus, foxes do not range arbitrarily in the enclosure but orientate themselves along structures.

The cover structures, on the other hand, were distributed throughout the entire enclosure. The foxes shifted their use of sectors depending on the location of the cover structures, but did not show preference for the respective sectors ahead of the rest of the enclosure. Cover structures are used for concealment when there is a threat (Weber & Meia 1996; Gloor 2002). The test enclosure contained a diversity of permanent natural structures, such as short hedges consisting of small fir trees and bushes, two dead trees, and several resting and hiding places above ground. Most of the structures could not be moved, either as a result of being too large (such as the dead trees) or because they had been planted, such as the small fir trees or bushes. It was almost certainly the case that permanent structures interfered with the experimental cover structures, such that the attractiveness of the experimental structures was relatively low. After completing data collection, the experimental structures were left in the enclosure, and over time trails were established through cover structures resembling trails found in the wild (C Kistler, personal observation 2007). This suggests that a longer period of habituation to the cover structures might have resulted in more intense usage.

Long structures are used to move along and also serve as barriers against humans and conspecifics (Blaney & Wells 2004; Aschwanden *et al* 2009). Foxes have a great fear of humans and tend to avoid them wherever possible (Lucherini *et al* 1995). Urban foxes would appear to have adapted to the presence of humans, but nevertheless show a preference for locations where human activity is low (Gloor 2002). Therefore, retreat and hiding places should be provided in captivity (Carlstead 1991; Nimon & Broom 2001). In combination, long structures and cover structures may allow foxes to safely explore their environment and forage for food. After introduction into the large, new enclosure, a strong preference was shown for similar structures from the very beginning. These results support the hypothesis that species living in cover-rich habitats benefit from enclosures with adequate structural enrichment.

It has been shown that housing conditions affect brain development and behaviour (Würbel 2001). The foxes had been raised as cubs in the test enclosure that had been richly structured in order to provide a stimulating environment and enable the development of normal behaviour. Feeding enrichment was provided which proved to enhance behavioural diversity and activity (Kistler *et al* 2009). The success of this environmental enrichment is reflected in the fact that none of the four individuals developed behavioural abnormalities, such as stereotypies, either in the test enclosure or in the new enclosure.

Effects of structural enrichment on activity

The foxes did not show enhanced activity in treatments with experimental structures present. However, activity levels were high during both experiments. This could have been because the test enclosure was furnished, in addition to the experimental structures, with various other natural structures. Therefore, shelter and hiding places were always in close proximity when the foxes were moving throughout the enclosure. The reduced activity during the final treatment in the experiment on cover structures (cLOC 1e) was probably a direct result of road construction work being carried out nearby. Nevertheless, the foxes selectively used the experimental cover structures during this period when they were ranging in the enclosure.

The newly built, natural-looking enclosure spanned 4,000 m^2 and was larger than the test enclosure in which the foxes grew up by a factor of 13. Distances between structures were longer, and more open space was available. As expected, the foxes used the structures selectively and showed pronounced preferences for areas containing structures compared to corresponding structure-less areas. In the course of the three-week observation period, all four individuals showed increased use of open space and increased activity. In the new enclosure, individual activity levels after three weeks were comparable to individual activity levels in the previous test enclosure. In both enclosures, feedings were comparable. Since in the test enclosure and in the new enclosure, respectively, food was provided at several alternating sites every day, the foxes had to search for food and, therefore, finding food was time consuming. The increase in activity correlated with a less-pronounced preference for areas containing structures. This suggests that in a new and therefore potentially threatening situation, structural enrichment assumes great importance. Furthermore, even when foxes were more familiar with their new environment, they still appeared to prefer areas containing structures, although this preference was less pronounced.

Increased use of cover structures and lower activity levels after the transfer of the foxes might reflect a novelty effect. However, also after three weeks, the foxes mainly used one of the structures to rest. Only rarely did they rest in open space. This would suggest that structural enrichment was important not only in the new situation following the transfer, but also when the enclosure became more familiar to the foxes. Therefore, the high percentage of cover-structure usage appeared to reflect a preference for structures by the foxes and cannot be fully explained by a novelty effect. The interpretation of our results is also supported by other studies which attribute abnormal behaviours to the lack of secure hiding places (Carlstead 1991; Nimon & Broom 2001).

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We did not measure any physiological correlate of stress. Nevertheless, we suggest that increased activity indicates improved well-being because structural enrichment enables animals to explore the enclosure and forage for food more safely. Red foxes are known to decrease activity levels when they are disturbed by human activity and shift their activity to more tranquil areas and those with dense cover (Cavallini & Lovari 1991; Gloor 2002; White *et al* 2006). Wild foxes are active not only during the night but also throughout the day, but mostly in areas where there is not much human activity (Zabel & Taggart 1989; Cavallini & Lovari 1991; Ricci *et al* 1998), and they tend to prefer to move in cover-rich habitats (Lucherini *et al* 1995). In the wild, foxes repeatedly rest during their active periods (Weber *et al* 1994; Doncaster & Macdonald 1997) and use different resting sites (Furrer 1999; Marks & Bloomfield 2006; White *et al* 2006). Hence, structural enrichment was placed in such a way that the foxes were always able to retreat and hide or move along a nearby structure while ranging. Our results indicate that a net-like arrangement of structural enrichment, including cover and long structures, is likely to be the most adequate furnishing to influence enclosure use.

Animal welfare implications

Previous studies have shown that stereotypies and other abnormal behaviours occur frequently in captive animals and can have a detrimental effect on welfare (for a review see Mason *et al* 2007). Such behavioural disturbances arise when enclosures lack critical resources and stimuli that facilitate species-typical behaviour (Mason 1991). Mason *et al* (2007) regard environmental enrichment as the most adequate means to solve these problems. Adequate environmental enrichment can be identified and tested by using the type of naturalistic approach applied in this study. Providing captive animals with a richly structured environment and an adequate feeding enrichment (eg Kistler *et al* 2009) throughout their life may be crucial because housing conditions affect brain development and behaviour (Würbel 2001). The development of normal behaviour is most important for animals bred for reintroduction in conservation programmes (Rabin 2003), but also for the well-being of captive animals in general.

Conclusion

In captivity, structural enrichment has proven important for species that live in cover-rich habitats and suffer high risks of predation (Ödberg 1987; Buchwalder & Wechsler 1997; Wiedenmayer 1997; Würbel *et al* 1998). Therefore, to establish a species-adequate enclosure, the natural environment the species has evolved in has to be taken into consideration. Providing red foxes with elements simulating natural structures, such as hedges or thickets had a profound effect upon their use of the enclosure. All individuals showed a preference for moving along long wooden structures and shifted their use of sectors depending on the location of cover structures. However, permanent structures in the enclosure which also provided cover and hiding places probably interfered with the use of experimental cover structures. Also, in the new enclosure, the foxes showed a significant overall preference for structures and a preference for sectors containing structural enrichment compared to corresponding areas with no structural enrichment. In conclusion, both cover and long structures are important in enclosures that aim at providing captive foxes with a species-adequate environment. In combination, they may meet the ecological and behavioural needs of an opportunistic carnivore.

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