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Feeding enrichment in an opportunistic carnivore: The red fox

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ABSTRACT

In captive carnivores, species-specific behaviour is often restricted by inadequate feeding regimens. Feeding live prey is not feasible in most places and food delivery is often highly predictable in space and time which is considerably different from the situation in the wild. As a result, captive carnivores are often inactive, show little behavioural diversity and are prone to behavioural problems such as stereotypic pacing. Using artificial feeding devices to substitute for natural food resources is a way to address these problems. In a group of four red fox (*Vulpes vulpes*), we compared a conventional feeding method to four different methods through the use of feeding enrichment that were based on natural foraging strategies of opportunistic carnivores. Feeding enrichments consisted of electronic feeders delivering food unpredictable in time which were successively combined with one of the three additional treatments: a self-service food box (allowing control over access to food), manually scattering food (unpredictable in space), and an electronic dispenser delivering food unpredictably both in space and time. The aim of administering feeding enrichment in this study was to stimulate appetitive (food searching) behaviour and to increase time spent in feeding. Compared to conventional feeding, diversity of behaviour and overall activity were significantly enhanced in the presence of electronic feeders in all four foxes (EF > CON1 = CON2, EF + SF > CON1 = CON2, EF + MS > CON1 = CON2, EF + ED > CON1 = CON2). Behavioural diversity was highest when the foxes had control over access to food (EF + SF), while the manual scattering of food (EF + MS) and the electronic dispenser (EF + ED) enhanced food searching behaviour. These results indicate that in opportunistic carnivores natural foraging and feeding behaviour can be stimulated by simple feeding enrichment strategies, and that foraging behaviour is stimulated most when food delivery is unpredictable both in space and time.

1. Introduction

There is increasing concern over the welfare of zoo animals, and animal welfare has become a central issue in zoo biology (Mason et al., 2007). Enclosures of wild animals in zoos and wildlife parks are often designed to mimic the animal's natural habitat (Robinson, 1998). Whether the illusion also satisfies the animals' behavioural needs, however, is often unclear. Zoo enclosures should provide wild animals with stimulating environments (Markowitz, 1982) to facilitate species-typical behaviour and to prevent abnormal behaviours. Consequently, 'naturalness' of behaviour and absence of abnormal behaviours are often used as proxy measures of good welfare. In particular, the more of its species-typical behavioural repertoire an animal can

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express, the better the enclosure is assumed to satisfy the animal's behavioural needs (Markowitz and LaForse, 1987; Shepherdson et al., 1993; Bashaw et al., 2003; Wechsler, 2007). 'The ability to perform most natural patterns of behaviour' is also one of the essential five freedoms listed by the Farm Animal Welfare Council (1993). However, others have argued that naturalness of behaviour is a poor measure of animal welfare (Dawkins, 2006). Indeed, not all behaviours seem essential for the well being of captive animals, as for example escaping from a predator, infanticide, or coping with natural obstacles (Hughes and Duncan, 1988; Veasey et al., 1996; Stauffacher, 1998; Dawkins, 2006).

Foraging behaviour is undeniably an essential part of all animals' lives. Under natural conditions, animals often spend most of their active time searching for food, as foraging is generally time consuming and the animals' activity phases are adapted to the foraging needs imposed by their habitats (Herbers, 1981; Shepherdson et al., 1993). In wild carnivores, the availability of food is typically unpredictable both in space and time, so they have to use specific skills to locate and exploit food resources. In contrast, feeding of captive carnivores is often predictable in space and time, and foraging is limited to food intake. Therefore, feeding enrichment based on the animals' natural foraging strategies may be crucial for the well being of captive carnivores (Lindburg, 1998; Bashaw et al., 2003).

Depending on their food spectrum, carnivores use a variety of foraging strategies. Foxes (*Vulpes* sp.) are opportunistic carnivores with a wide trophic niche. They exploit various food sources of which vegetables or fruit can make up a large part (Lucherini and Crema, 1994). Such food is persistently searched for, and sometimes skilfully exploited, especially by animals living in or near settlement areas (Contesse et al., 2004). Thus, feeding enrichments may be particularly beneficial to opportunistic carnivores such as captive foxes.

Previous work in captive carnivores has used a variety of feeding enrichment strategies. Artificial moving prey elicited natural hunting behaviour in servals (*Felis serval*) and cheetahs (*Acinonyx jubatus*) (Markowitz and LaForse, 1987; Williams et al., 1996). In European wildcats (*Felis s. sylvestris*) automatic electronic feeders elicited natural hunting behaviour and prevented behavioural disturbances (Hartmann-Furter, 2000), whereas feeders which had to be opened by margays (*Leopardus wiedii*) did not elicit appetitive behaviour (Gusset et al., 2002). In tigers (*Panthera leo*), stereotypic behaviour was decreased by manipulable feeders (Jenny and Schmid, 2002). In lemurs (*Eulemur fulvus albifrons*, *Hapalemur griseus*) overall activity and locomotor behaviour was increased when food was offered in self-service food boxes (Sommerfeld et al., 2006). Hiding food in the enclosure reduced stereotypic behaviour in black bears (*Ursus americanus*) and increased searching behaviour in bush dogs (*Speothos venaticus*) (Carlstead et al., 1991; Ings et al., 1997).

Based on these findings, we studied four different feeding enrichments in a group of four red foxes housed in a near-to-natural outdoor enclosure to test for their effects on foraging and feeding activity and on behavioural diversity compared to conventional feeding. We hypothesised that the foxes would be most active and their behaviour most diverse, when food was presented unpredictably in space and time, and when it was most difficult (time consuming) to find. To test this hypothesis, we varied foraging demand and predictability of food in space and time by using electronic feeders (food unpredictable in time) either (i) alone or in combination with (ii) a self-service food box (unpredictable in time plus time-consuming manipulation), (iii) scattered and hidden food (unpredictable in time and space plus time-consuming), or (iv) an electronic dispenser (highly unpredictable in time and space plus time consuming). We predicted that general activity and behavioural diversity would increase from treatment (i) through treatment (iv).

2. Materials and methods

2.1. Subjects and housing

The study was conducted between March and June 2005 in an outdoor enclosure at Langenberg wildlife park near Zürich, Switzerland. The enclosure was not accessible to visitors, but designed as a test enclosure for a new exhibit planned for foxes in the public part of the park.

The study subjects formed a group of four adult red foxes, two males and two females, which were unrelated to each other. All had been found as cubs in 2002, and had since lived together in the test enclosure. 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 resting places of different kinds, shrubs, hedges composed of small fir-trees, trees suitable for climbing, heaps of stones and earth, a wooden den and two artificial dens. Interference in dens by humans never occurred during the observation periods in order to provide the animals with a secure place to retreat.

2.2. Feeding treatments

The foxes were fed daily except on Saturdays when they fasted. In all feeding treatments, the daily diet consisted of 400 g of meat (freshly killed rats or small pieces of meat), 200 g of fruits, and 200 g of dried dog food, raisins, sunflower seeds and nuts.

Five different feeding treatments were used throughout the study.

- In feeding treatment one (conventional, CON), all food was given at once always at the same time (0930 h) and in the same place. Food supply was therefore predictable in time and space.
- In feeding treatment two (electronic feeders, EF), three computer-controlled electronic feeders (Hartmann-Furter, 2000) were located at three different sites (separated by approx. 10 m) inside the enclosure. Each of the three feeders contained one third of the meat ration, two feeders additionally contained fruits, dried dog food, raisins, sunflower seeds and nuts. From the feeder with meat only, food was catapulted out of the food box when the shutter opened because the food was tied to an elastic cord fixed to the branch of a nearby tree. The other two feeders dropped the food down to the ground upon opening the shutter. Each feeder was opened once every day and opening times were randomly distributed over the day between 10:00 h and 18:00 h. Food supply was therefore predictable in space, but unpredictable in time.
- In feeding treatment three (electronic feeders plus self-service food box, EF + SF), a wooden self-service food box was installed in addition to the three electronic feeders. The box was held 80 cm above the ground by a rope attached to a pole, and was filled with nuts, dried dog food and sunflower seeds (25% of the daily diet). Upon manipulating a handle, the food inside the box fell through a small whole to the ground. The remaining food was distributed across the three electronic feeders, which were operated as described above. Therefore, food supply was again predictable in space, with 75% of the food supply being unpredictable in time, and 25% of the food supply being accessible by performing a specific manipulation.
- In feeding treatment four (electronic feeders plus manually scattered and hidden food, EF + MS), 100% of nuts, dried dog food, raisins and sunflower seeds, 20% of meat, and 50% of fruits were manually scattered

and hidden in the enclosure. 80% of the meat and 50% of the fruits were distributed across the three electronic feeders, which were operated as described above. Thus, about half of the food supply was predictable in space, but unpredictable in time, while the other half was unpredictable both in space and time and, therefore, required additional foraging time.

- In feeding treatment five (electronic feeders plus electronic dispenser, EF + ED), an electronic dispenser was installed in addition to the three electronic feeders. The dispenser consisted of a plastic tub, with a distributor placed inside to partition the food into small portions and an analogue timing device. The mechanism activating the distributor was started by the timer. On activation, the distributor released a small amount of food, which fell onto a fast rotating disk and from there was dispersed within a radius of about six metres from the dispenser. The device was filled with nuts, dried dog food and sunflower seeds (25% of the daily diet). It was placed at the same location as the self-service food box and food was provided in eight portions every day at times that were different from the times when the electronic feeders released food. The electronic feeders were filled with the remaining 75% of meat, fruit and raisins. This treatment provided the highest degree of temporal and spatial unpredictability, and like treatment four (EF + ED) required additional foraging time.

Throughout the study, food was placed inside the different devices half an hour before the observation started in the morning.

2.3. Experimental design and data recording

The foxes were presented with the four different feeding enrichments in a fixed order: EF, EF + SF, EF + MS, and EF + ED, and conventional feeding was presented before (CON1) and after (CON2) the feeding enrichments. Each of the six treatments lasted two weeks. The first week was used to habituate the foxes to the new feeding treatment. During the second week, data were collected on five days for four hours each day from 10:00 to 11:00 h, 12:00 to 13:00 h, 14:00 to 15:00 h and from 16:00 to 17:00 h. Behavioural data were collected by direct observations from an elevated hide with the aid of binoculars. The foxes were used to the observer's presence on the hide.

Prior to the study, *ad libitum* sampling over a period of 14 days served to establish a detailed ethogram that was complemented by information from the literature (Tembrock, 1957, 1982). All behaviours were grouped into one of eleven functional categories: exploration, monitoring, food searching, food-acquisition, feeding, resting, escape behaviour, other forms of locomotion (walking, trotting, gallop and jumping), comfort behaviour, social behaviour (socio-positive and socio-negative), and social behaviour during feeding bouts. Stereotypic behaviour or extended aggression did not occur during these pilot observations.

During the main study, focal animal sampling was used to assess behavioural diversity, while general activity was assessed using scan sampling. Thus, during each observation hour, each fox was continuously observed during six consecutive periods of 2.5 min (in total 15 min), whereby each behaviour was recorded only once. The order in which the four individuals were observed was kept the same throughout the day but was randomised between days. In addition, instantaneous observations at 2.5 min intervals were conducted to scan general activity. Activity was defined as all behaviours except resting and sleeping.

2.4. Data analyses

To quantify behavioural diversity, the number of behaviours per functional category was summed up over the total observation time per feeding treatment. Based on these numbers, the Shannon index of diversity H (Shannon and Weaver, 1949) was calculated as

$$H = -\sum(p_i \ln p_i),$$

where p_i is the relative abundance of each functional category, calculated as the proportion of behavioural elements of a given functional category to the total number of behavioural elements of all functional categories: n_i/N. The index was calculated per feeding treatment and per individual. It increases with increasing numbers of functional categories, and as the relative representation of each functional category becomes more even. Lower indices represent lower behavioural diversity. To quantify activity, the number of active behaviours was summed up over total observation time per feeding treatment and per individual, and the proportion of active behaviour was calculated. To establish time budgets, behaviours of functional categories were summed up per hour and per feeding treatment for all individuals. Functional categories were combined into the following main categories: Exploration (locomotion, exploring, monitoring), food (food searching, food acquisition, feeding, social food), other (comfort, escape, and social behaviour), and resting. Overall mean percentage of main categories was calculated per feeding treatment.

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

3. Results

3.1. Effects of feeding enrichment on behavioural diversity

Diversity of behaviour differed significantly between feeding treatments ($\chi^2 = 15.571$, $p = 0.001$, df = 5, $n = 4$; Fig. 1), with the lowest indices found during the first conventional feeding. Behavioural diversity was increased during all enriched feeding treatments, and declined again during the final conventional feeding. Peak median diversity occurred during the treatment allowing for self manipulation of access to food (EF + SF). Post-hoc comparisons revealed that all feeding enrichments differed significantly from both the conventional feeding treatment presented in the beginning and at the end of the experiment (EF > CON1 = CON2, EF + SF > CON1 = CON2, EF + MS > CON1 = CON2, EF + ED > CON1 = CON2). Furthermore, the diversity index in the EF + SF treatments was significantly higher than in the three other feeding enrichments (all differences $p \leq 0.05$). All four individuals showed the same pattern over the course of the experiment.

3.2. Effects of feeding enrichment on activity

Overall activity differed significantly between the different feeding treatments ($\chi^2 = 16$, $p = 0.001$, df = 5, $n = 4$; Fig. 2), with the lowest activity found during the first conventional feeding treatment. Activity was increased during feeding enrichment treatments, and decreased again during the final conventional feeding. Peak median activity occurred during the treatment when food presentation was most unpredictable in time and space (EF + ED). Post-hoc comparisons revealed that all feeding enrichments differed significantly from both the conventional feeding treatment at the beginning and at the end of the experiment (EF > CON1 = CON2, EF + SF > CON1 = CON2, EF + MS > CON1 = CON2, EF + ED > CON1 = CON2). Furthermore, activity during EF + SF was significantly lower than during EF + MS and EF + ED (EF + SF < EF + MS = EF + ED).

Fig. 3 shows the activity budget of the group during feeding treatments. During CON1 and CON2, active mean time spent was 14% and 26%, respectively. Exploration and food related behaviour increased during all four enriched feeding treatments. Mean percentage of exploration ranged between 21% during EF + SF and 29% during EF and EF + ED. Mean percentage of food related behaviour increased continuously from 10% during EF to 22% during EF + ED. Other behaviours (comfort, flight and social behaviour) increased during EF, EF + SF, and EF + MF, but decreased again during EF + ED.

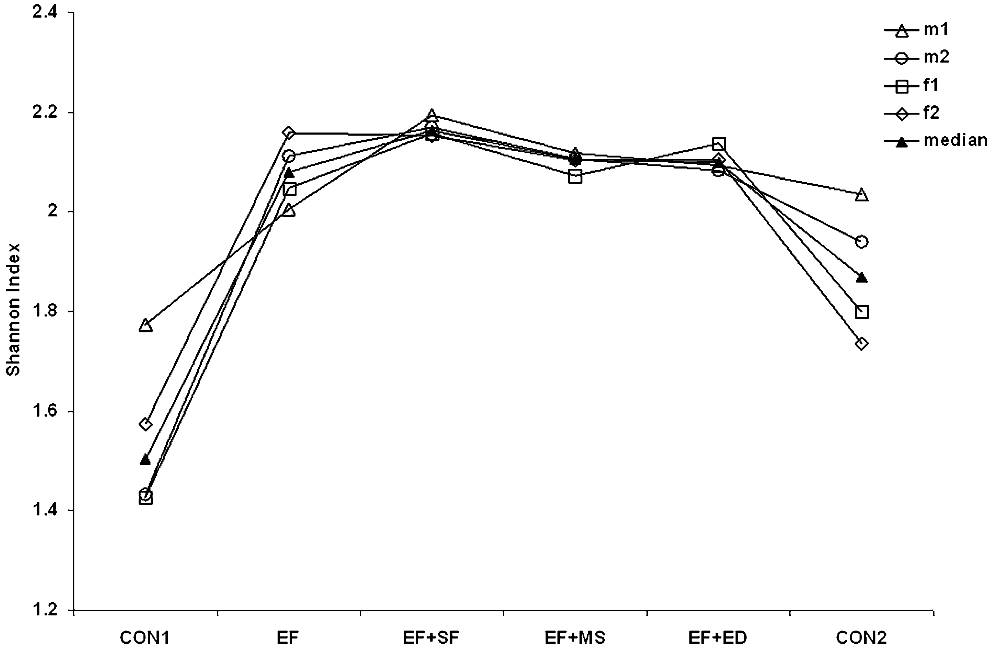

Fig. 1. Individual behavioural diversity during conventional feeding and different feeding enrichment treatments. Values of Shannon diversity index of four red foxes (two males, m1, m2, and two females, f1, f2) and overall median are shown. Lower indices represent lower behavioural diversity, and higher indices represent higher behavioural diversity. EF = electronic feeders, SF = self-service food box, MS = manually scattered and hidden food, ED = electronic dispenser. CON1 and CON2 = conventional feeding before and after feeding enrichments, respectively.

4. Discussion

Consistent with our predictions, all four feeding enrichments significantly enhanced individual behavioural diversity and activity of the four red foxes compared to a conventional feeding treatment. Our findings indicate that any kind of temporal and/or spatial unpredictability in the presentation of food has a stimulating effect on the foxes' behaviour.

In all enriched feeding treatments, behavioural diversity was increased in all functional categories, except resting. Behavioural diversity was highest when the foxes were able to manipulate access to food (EF + SF). However, three of the four foxes showed the highest absolute numbers of behavioural elements when the spatial and temporal unpredictability of food was highest (EF + ED). Unpredictability of feedings can cause enhanced abnormal or agonistic behaviour prior to feedings (Waitt and Buchanan-Smith,

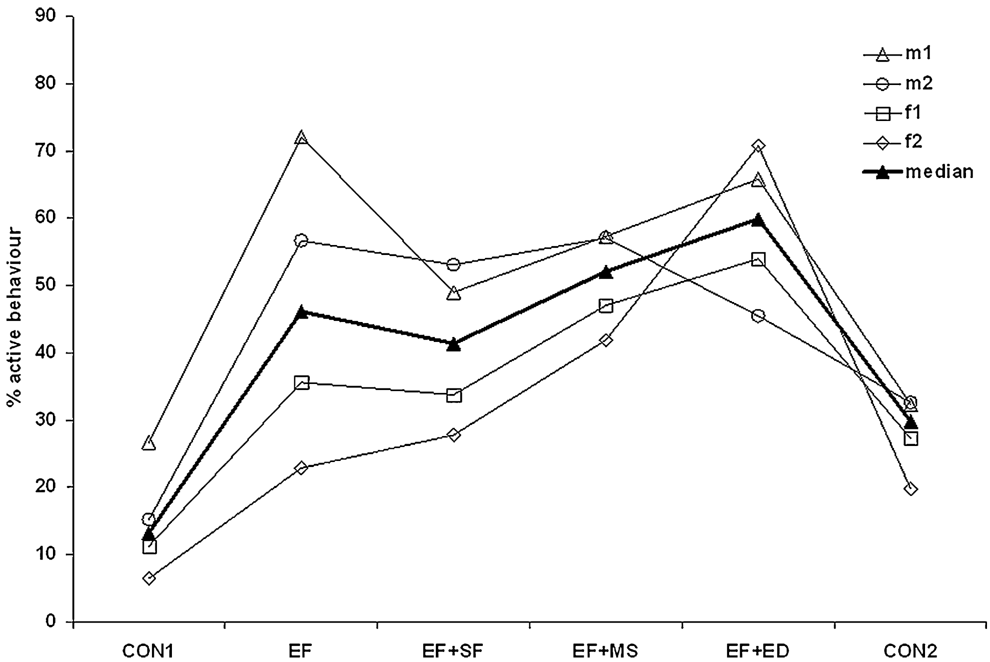

Fig. 2. Activity (% of observation time) of four red foxes (two males, m1, m2, and two females, f1, f2) during conventional feeding and different feeding enrichment treatments, EF = electronic feeders, SF = self-service food box, MS = manually scattered and hidden food, ED = electronic dispenser. CON1 and CON2 = conventional feeding before and after feeding enrichments, respectively.

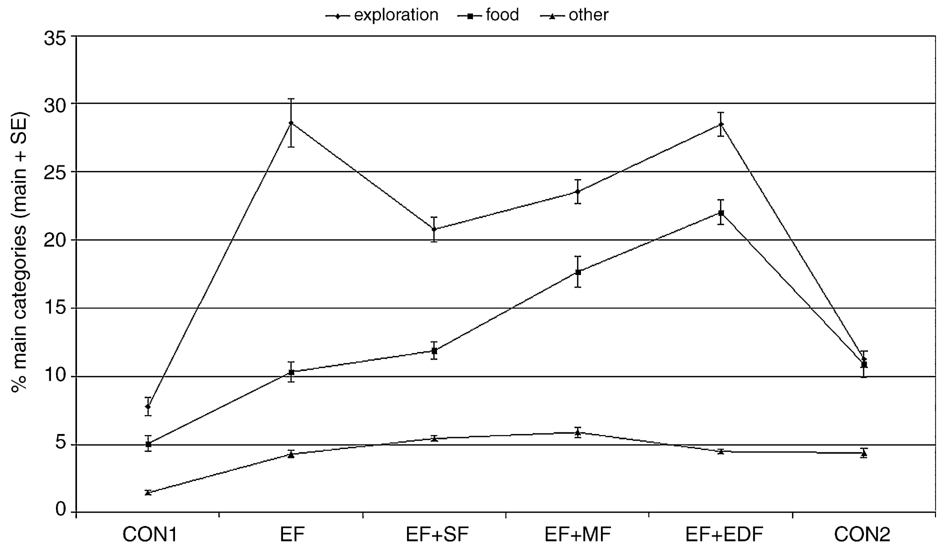

Fig. 3. Activity budget (overall mean + SE) of the fox group during conventional feeding and feeding enrichment treatments. Main categories are exploration (locomotion, exploration, monitoring), food (food searching, food acquisition, feeding, social food), other (comfort, escape, and social behaviour). EF = electronic feeders, SF = self-service food box, MS = manually scattered and hidden food, ED = electronic dispenser. CON1 and CON2 = conventional feeding before and after feeding enrichments, respectively.

2001). It is assumed that this is connected with unreliable signals caused by caretakers. As in this study feeding times were not linked to the caretakers' presence no external unreliable signals occurred. The foxes never showed any signs of behavioural disturbances such as stereotypes or extended aggression. Thus, all feeding enrichments induced higher activity and a greater diversity of behaviour without causing behavioural problems. Since the diurnal pattern of activity of wild red foxes varies greatly depending on the diurnal pattern of food availability (Zabel and Taggart, 1989; Cavallini and Lovari, 1991; Ricci et al., 1998) and human activity (Lucherini et al., 1995; Gloor, 2002), feeding enrichment during daylight hours appears to be an adequate form of enrichment in red foxes.

During both the initial and final conventional feeding treatment, resting was high in all four foxes. Providing food once daily at a particular time is common in zoos and wildlife parks due to operating schedules (Carlstead, 1991; Carlstead et al., 1991; Shepherdson et al., 1993; Hartmann-Furter, 2000). In our study animals, this treatment hardly stimulated any food searching behaviour. General activity was considerably higher in all feeding enrichments. While the type of feeding enrichment did not affect levels of general activity, however, the proportion of food related behaviour such as food searching or food acquiring increased the most during the feeding treatment with the highest spatial und temporal unpredictability (EF + ED). Here, the foxes repeatedly browsed the enclosure. Furthermore, food items such as nuts, sunflower seeds and dog food are of small size, and finding them in the natural vegetation is time consuming. Along with food related behaviour there was an increase in exploratory behaviour such as locomotion and monitoring behaviour. The least amount of exploratory behaviour was elicited when the foxes had control over access to food items concentrated in a self-service food box (EF + SF). Although food related behaviour such as manipulative food acquiring behaviour increased, the foxes were less active compared to treatments when food was provided spatially and temporally unpredictable (EF + MS, EF + ED).

Because the four foxes belonged to one group, we could not randomise the order of feeding enrichments across individuals. Therefore, the trend towards increased exploration and food related behaviour with increasing unpredictability of food presentation is confounded by test order. However, the foxes adapted quickly to feeding conditions during the habituation weeks before data were collected and no differences were found in the foxes' responses to the first and last conventional feeding regime. Therefore, it is unlikely that the differences between feeding treatments are explained by test order effects alone. Furthermore, the four subjects may have influenced each other in their behaviour. However, foxes are solitary foragers and do not monopolise food resources (Macdonald, 1988). Therefore, our findings are likely to generalise beyond this specific study group.

In accordance with other studies on feeding enrichment in captive carnivores (e.g. Carlstead et al., 1991; Hartmann-Furter, 2000; Bashaw et al., 2003; Sommerfeld et al., 2006), our results indicate that feeding enrichments based on natural activity patterns and feeding strategies can effectively stimulate species-specific behaviour. Increased activity and behavioural diversity induced by feeding enrichments are also likely to reflect improved well being, although independent evidence based on more direct measures of well-being is needed to confirm this.

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