JZAR www.jzar.org JOURNAL OF ZOO AND AQUARIUM RESEARCH

JZAR Research article

OPEN ACCESS

Research article

Automated scatter-feeding increases foraging activity of zoo-housed meerkats *Suricata suricatta* to durations observed in the wild and elicits sentinel behaviour during feedings

Ida Bähler[1,2], Karin Federer[3], Leyla R. Davis[4], Sebastian Weber[4], Anita Burkevica[2], Sebastian Schneider[5], Paul Dierkes[5] and Marcus Clauss[1]

[1]*Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Switzerland*
[2]*Parken Zoo, Eskilstuna, Sweden*
[3]*Walter Zoo Gossau, Switzerland*
[4]*Zoo Zurich, Switzerland*
[5]*Faculty of Biological Sciences, Goethe University, Frankfurt am Main, Germany*

Correspondence: Marcus Clauss, email; mclauss@vetclinics.uzh.ch

Keywords: activity budget, diet, enrichment, feeding, foraging, meerkat

Article history:
Received: 01 Mar 2024
Accepted: 29 May 2024
Published online: 31 Jul 2024

Abstract

Food-based environmental enrichment such as scatter-feeding is an important strategy to augment animal welfare in zoos. However, manually scattering food around an enclosure is time-consuming. Automatic scatter feeders could be an important tool to help implement better feeding strategies. This study hypothesised that a scatter-feeding regime would stimulate more natural feeding behaviours in meerkats *Suricata suricatta* and animals were expected to show more active foraging and less food monopolising behaviour compared to conventional lump feeding. Meerkat groups in three zoos were studied. The feeding regime of each meerkat group was manipulated over a total of five weeks in an A-B-A-B-A scheme, two scatter-feeding regime (B) weeks were interspersed with three lumped feeding regime (A) weeks. During scatter-feeding sessions, animals showed more foraging and less food monopolising behaviour, as well as being more active and visible overall than during lumped feeding sessions. The overall foraging behaviour of zoo-housed animals during scatter-feeding (36% of the total daily activity) was nearly identical to that reported for free-ranging animals (37% of the total daily activity). In two of the three zoos, individuals were observed to perform sentinel (or guarding) behaviour during feeding bouts under the scatter-feeding regime, a natural behaviour not observed during lump feeding. The results show that automatic scatter-feeding is a viable and effective tool to improve indicators of welfare in meerkats and potentially other animals.

Introduction

Zoos are moving away from provisioning animals with their daily diet in a single easily accessible portion in favour of implementing food-based environmental enrichment (EE) based on “devices that require manipulation to extract the food, or required behaviors to obtain food” (Maple and Perdue 2013). Food-based EE represents an important part of the overall EE concept (Riley and Rose 2020). There are indications that the opportunity to forage for food is a more effective enrichment strategy than introducing non-food enrichment objects (Cummings et al. 2007). Such strategies may use the hunting instinct, for example by providing food as a moving target or distributing food to animate motion (Kleinlugtenbelt et al. 2023). Thus, these modified feeding strategies represent an attempt to mimic conditions in the wild, where animals spend a significant proportion of their activity budgets hunting or foraging for food (Fens and Clauss 2024; Maple and Perdue 2013; Veasey et al. 1996).

However, EE can be very time consuming for zookeepers (Podturkin and Papaeva 2020) and resource constraints in this respect may limit the amount of EE provided to zoo animals. Therefore, automated mechanisms represent important tools for zoo animal husbandry if they effectively relieve keeper workloads. Several different automated feeding systems have so far been described. Feeding boxes may open at random intervals, requiring the animals to check their status regularly (Fischbacher and Schmid 1999; Jenny and Schmid 2002). A time-delay puzzle feeder indicated acoustically when the animal could manipulate it to extract food (Krebs and Watters 2017). Belt-feeders delivered food at different times in different parts of the enclosure (Charmoy et al. 2015; Watters et al. 2011). Feeding dispensers were stocked with live insects crawling unpredictably out of the storage object (Shepherdson et al. 1989). A type of machinery that is freely available commercially for animal feeding but is—to the authors' knowledge—only rarely implemented in zoos is the automatic scatter feeder. Such devices are used in commercial fish farming to spread food evenly over large areas enabling equal feeding of large numbers of animals, with better growth rates (Rad et al. 2004). They are also well known in hunting to supply bait food, e.g. to wild boars. For zoos, the authors are only aware of a report on the use of a scatter feeder similar to that used in the present study in red river hogs *Potamochoerus porcus* (Moore and Powell 2012), in grizzly bears *Ursus arctos horribilis* (Andrews and Ha 2014) and a recent description of an automated scatter feeder developed for great ape feeding (Jadali et al. 2023).

Insectivorous species might benefit particularly from this feeding method. These animals typically must acquire many individual comparatively small diet items in sufficient amounts to meet their energy demands, leading to a high proportion of their activity budget spent foraging. For example, foraging in European hedgehogs *Erinaceus europaeus* amounts to around 70% of their active time (Riber 2006). In meerkats *Suricata suricatta*, foraging activity also comprises the majority of their active period (Doolan and MacDonald 1996). They forage especially for insects, which comprise up to 78% of their prey items in the wild (Doolan and MacDonald 1996). While the group is foraging, usually one individual is on the lookout for predators (Clutton-Brock et al. 1999). This so-called sentinel behaviour is performed from an elevated position (Tatalović 2012).

The AZA husbandry guidelines (AZA Small Carnivore TAG 2011) state that "scattering diet items and/or multiple feeding stations are the most effective ways to feed a large group of meerkats". The text suggests that the "primary part of the diet should be fed in the morning, allowing animals to eat throughout the day. Whole prey items (e.g., mice, ribs) and live bugs (mealworms and crickets) can be fed in the afternoon/early evening or at scattered enrichment times" and recommends "they be offered the majority of their diet once daily, in the morning" because "if a schedule of multiple, small feedings is adopted the provision of less food more often may stimulate unnecessary aggression leading to social unrest." To the authors' knowledge, no sentinel behaviour during such few feeding sessions has been reported in the literature. Feeding the daily diet a restricted number of times may reduce the time meerkats spend foraging, leading to a discrepancy between free-ranging and zoo activity budgets.

A typical feature of the prey items of insectivorous predators is that they are so small that even when the animals forage in groups, an animal that finds a prey item can usually consume it directly without interference from conspecifics. If, by contrast, animals in zoos are offered food in large lumped portions, this may foster a rather unnatural condition of food competition, where food is monopolised against conspecifics, and aggression can occur (AZA Small Carnivore TAG 2011). Often (but not always), meerkats in zoos are fed several lumped food portions from food bowls with diet items too large for immediate swallowing (such as rodents, day-old chicks, quails or even fish) that require multiple bites for consumption (AZA Small Carnivore TAG 2011; I. Bähler and M. Clauss personal observation). This regularly leads to protective behaviour, guarding the food against conspecifics, often including constant movement where the 'owner' of a diet item positions itself between the item and a conspecific (I. Bähler and M. Clauss personal observation). Correspondingly, most aggressions between zoo-housed meerkats have been reported to occur during feeding times (Tomczyk and Zieliński 2021). That meerkats are not adapted to share resources has also been demonstrated experimentally (Amici et al. 2017).

One reason for reluctance to adopt a scatter-feeding regime might be hygiene considerations. These can apply to concerns about how the machine itself can be cleaned. Additionally, this is relevant should scattered feed and animal faeces get mixed in the enclosure. Concerns about hygiene apply in particular to animals kept in groups and have been raised especially in birds, for example in pigeons (Waters and Smeeton 2002) and broilers (Riber et al. 2018). Meerkats reliably defecate in latrines (Jordan et al. 2007), offering the option of setting the scatter device to cover an area that excludes these latrines to reduce the risk of mixing food and faeces.

This study hypothesised that a scatter-feeding regime provides more natural meerkat feeding conditions by scattering an extruded or pelleted food consisting of very small units over a large area of the enclosure many times during the day. Increased foraging activity and an elimination of food monopolising behaviours was expected, as these items are small enough to be eaten directly. To evaluate the two different regimes, corresponding behaviours exhibited by meerkats in three different zoological institutions were analysed.

Material and methods

Animals and husbandry

Three meerkat groups were studied: two in Switzerland where this study was considered an animal experiment and permitted by the cantonal veterinary offices of St. Gallen and Zurich under national license no. 34582, and one in Sweden where observations of animals provided with an adequate diet for scientific purposes is not considered an experiment that requires licensing.

First, a group of 12 individuals, including an alpha female, two males and their adult and juvenile offspring was studied at the Walter Zoo in Gossau, Switzerland in the spring of 2022. A second group of 19 individuals, consisting of a female and two male brothers, as well as their adult and juvenile offspring, were studied at Zoo Zurich in Zurich, Switzerland in autumn 2022. Finally, a group of six older individuals (five males, one female) aged five to eight years that had not produced offspring for many years were studied at the Parken Zoo in Eskilstuna, Sweden in the winter of 2022–2023.

At Walter Zoo, meerkats were kept primarily in an indoor enclosure area of 95 m^2 (Figure 1) and the scatter machine was placed centrally in this indoor enclosure. Weather permitting (above 12°C), the animals had access to an outdoor area. The flooring consisted of ferruginous sand with three hollowed-out hills as hiding places and a tunnel system built by the meerkats themselves, which extended over half of the enclosure. Various bushes and one big tree stump provided vantage points for the meerkats to observe their surroundings. A small pond in the middle of the enclosure provided a drinking station. The latrine area was in a corner next to the visitor area. Three African spurred tortoises *Centrochelys sulcata* lived in the same enclosure and were fed hay for ad libitum consumption and salad once daily in the early afternoon.

At Zoo Zurich, animals had unlimited access through cat flaps to two outdoor enclosures (110 and 30 m^2; Figure 2) and a third covered outdoor enclosure (25 m^2) was opened every afternoon for feeding insects together with visitors. An indoor enclosure (38 m^2) was permanently accessible to the animals and contained two small drinking stations. The tunnelling substrate was a solidifying sand (a mix of clay and sand) in which the animals could create

http://doi/org/10.19227/jzar.v12i3.828

Figure 1. Indoor enclosure of 12 meerkats *Suricata suricatta* and three African spurred tortoises *Centrochelys sulcata* at the Walter Zoo Gossau during spring 2022

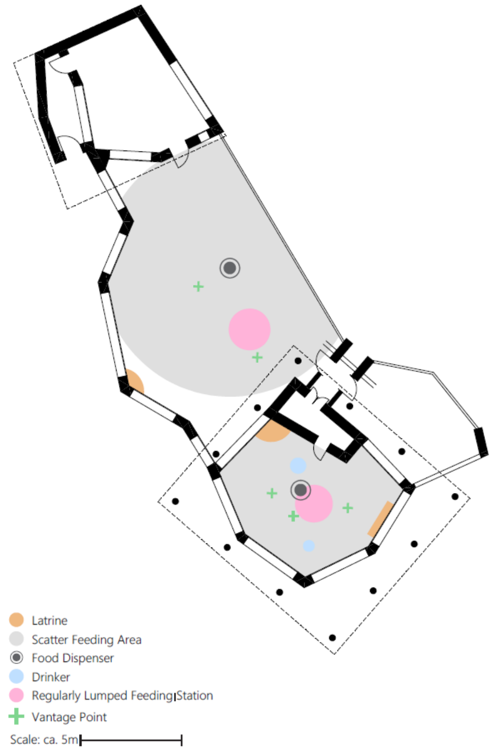

Figure 2. Indoor enclosure (bottom square) and three connected outdoor enclosures of 19 meerkats *Suricata suricatta* at the Zurich Zoo during autumn 2022

their own passage systems. Natural shrubs and planted trees were provided as well as replicated termite mounds. Several latrines were adopted across the different enclosures. Two scatter machines were installed. Weather allowing, one was used outdoors. When it rained, both machines were used indoors.

At Parken Zoo Eskilstuna, there were two indoor enclosures (50 m^2 and 13 m^2) connected by a tunnel (Figure 3). The outdoor enclosure was not accessible to the animals during the entire experiment because it was in winter. A thin layer of sand in the larger enclosure and straw bedding in the smaller enclosure lined the flooring. The enclosures were structured with tree trunks and artificial hollow rocks, moved daily by the keepers to provide a change of enclosure structure. One main latrine was adopted in one corner and there were two drinking spots. The scatter machine was located in the centre of the larger enclosure.

In the Walter Zoo and Zoo Zurich 'animal encounters' offered visitors an opportunity to feed the animals under supervision by a keeper. Here, care was taken to ensure that these were always carried out in exactly the same way, at the same time and same day, so that they did not become a changing component between feeding regimes but occurred consistently.

Study design

The experimental set-up was replicated in all zoos. The evaluation phase included five 4-day periods (i.e. a total of 20 days) per zoo. Animal feeding regimes were manipulated for a total of five periods, according to an A-B-A-B-A scheme. Two scatter-feeding

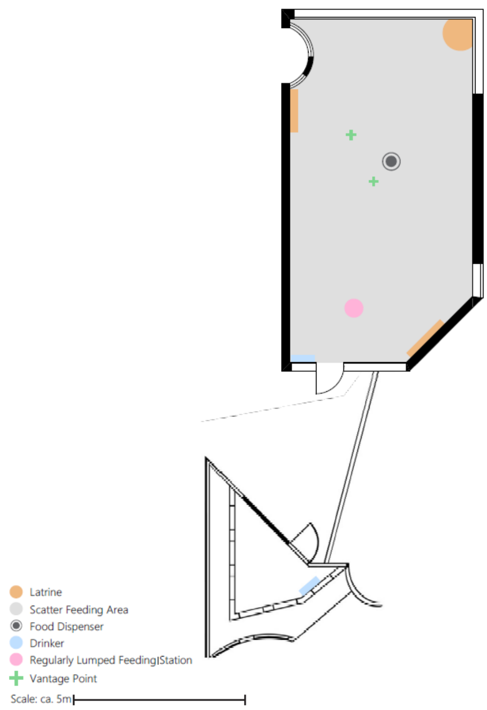

Figure 3. Two indoor enclosures for six meerkats *Suricata suricatta* connected with a tunnel at Parken Zoo Eskilstuna during winter 2023

periods (B) were interspersed with three periods of lumped feeding (A). For each of the five one-week periods, the animals were given the first three days to acclimatise to the respective feeding regime before behaviour recordings were made on days 4–7. Timing was chosen so that the recording days always took place during the working week (as opposed to weekends) to reduce the influence of larger visitor numbers (at Walter Zoo and Zoo Zurich; no visitors at Parken Zoo during the study period).

Diets

The diets in place at the respective zoos were used as the basis of the experimental diet regime, which required that feed that could be dispensed by the scatter machine composed a major part of the overall diet. Depending on the zoo, the animals also received other food items, including vegetables/fruits, whole animals such as day-old chicks or mice, dead or live insects and cooked eggs (Tables 1–3); these components changed during the course of a week.

Roughly, the daily diet consisted of 2/3 extrudates and 1/3 other food on an as-fed basis, where the amount of the diet was based on the amount of food the zoos fed their animals. At Walter Zoo and Zoo Zurich, the amount already fed was used, with proportionally more extrudates being added to the daily diet at the expense of the rest of the feed. At Parken Zoo, the animals were initially fed for ad libitum consumption. The amount of feed was slowly reduced prior to the actual experiment until no more remains were left.

The extrudate was required to be a complete feed of a size that the meerkats could pick up easily to reduce the possibility that the animals could steal food from each other; additionally, extrudates had to match the modified scatter feeder. At the Walter Zoo an extruded dry cat feed (Bitscat sterilised - duck and turkey, own brand Landi, Dotzingen, Switzerland) was used, as a more suitable extruded or pelleted insectivore feed that was compatible with the scatter machine could not be identified at the time. In the meantime, a dedicated insectivore extruded feed had been developed and marketed that was both palatable to meerkats and compatible with the scatter machine (3762 Insectivore extrudate, Granovit, Kaiseraugst, Switzerland). At Zoo Zurich, the meerkats were already fed with this product. At Parken Zoo, the animals were given several weeks before the study to get used to it by gradually increasing its proportion in the daily ration.

The animals received the same amount and kind of food on the same days of the week in both feeding regimes. Only the way the diet was offered changed (Tables 1–3).

Feeding methods

During lumped feeding, the daily diet for the whole group was either offered in three (Walter Zoo) bowls or one (Parken Zoo) bowl or scattered manually over two narrow areas of 2–3 m^2 (Zoo Zurich). The feeding frequency during lumped feeding was adjusted according to the usual feeding regime at the respective zoo—with three (Walter Zoo, Table 1), four (Zoo Zurich, Table 2) and one (Parken Zoo, Table 3) feedings per day; only at Zoo Zurich did this regime represent a reduction of the six manual scatter-feeding events habitually in place.

For automated scatter-feeding, a modified hanging food dispenser, model Feeder Compact X42 (Dörr GmbH, Neu-Ulm, Germany) was used, which scattered the food by centrifugation. The machine was originally developed for feeding game in a forest setting and was built for much larger quantities than the few grams needed for the meerkats. To reduce the amount of food dispensed at a time to the required amount, a 3D-printed item was inserted in the throw-off storage housing of the scatter machine to reduce the volume of the spinning dispenser and thus the amount of feed output to an appropriate level. Because test trials often resulted in a clogging of the machine, leading to frequent failure, a screw with two nuts was attached to one corner of the rotating part of the machine, creating an imbalance that led to vibrations of the device and thus reduced the probability of blockage. For a complete description of the changes made to the machine, including an .stl model of the inlet for 3D printing, see Supplementary Information 1.

The machine was installed at the positions designated in Figures 1–3, at a height that no animal could reach (higher than 60 cm) but low enough so that no feed was ejected over the enclosure

Table 1. Feeding schedules (per animal) at Walter Zoo

Time	Monday	Tuesday	Wednesday	Thursday	Friday	Saturday	Sunday
	Lumped feeding regime						
0900	10g vegetable 5 waxworms ¼ boiled egg	10g vegetable 4 Zophobas 10 mealworms	10g vegetable 5 grasshoppers	10g vegetable ¼ day chick 10 mealworms	10g vegetable 10 crickets	10g vegetable 10 crickets 7 earthworms	10g vegetable 10 crickets 8 earthworms
1200	11g cat pellets	11g cat pellets	11g cat pellets	11g cat pellets	11g cat pellets	11g cat pellets	11g cat pellets
1500	11g cat pellets	11g cat pellets	11g cat pellets	11g cat pellets	11g cat pellets	11g cat pellets	11g cat pellets
	Scatter feeding regime						
0900	10g vegetable 5 waxworms ¼ boiled egg	10g vegetable 4 Zophobas 10 mealworms	10g vegetable 5 grasshoppers	10g vegetable 1/4 chick 10 mealworms	10g vegetable 10 crickets	10g vegetable 10 crickets 7 earthworms	10g vegetable 10 crickets 8 earthworms
1030 to 1630 (13 times)	1.8g cat pellets	1.8g cat pellets	1.8g cat pellets	1.8g cat pellets	1.8g cat pellets	1.8g cat pellets	1.8g cat pellets

Pelleted food: Bitcats, Landi, Dotzingen, Switzerland (in % as fed: total ash 7.0, crude protein 32.0, crude fat 9.0, crude fibre 4.0)

http://doi/org/10.19227/jzar.v12i3.828

Table 2. Feeding schedules (per animal) at Zoo Zurich

Time	Monday	Tuesday	Wednesday	Thursday	Friday	Saturday	Sunday
	Lumped feeding regime						
0800	20g vegetable	20g vegetable	20g vegetable	20g vegetable	20g vegetable	20g vegetable	20g vegetable
1100	10g pellets	10g pellets	10g pellets	10g pellets	10g pellets	10g pellets	10g pellets
1300/1600	10g pellets	10g pellets	10g pellets	10g pellets	10g pellets	10g pellets	10g pellets
1300/1600	½ boiled egg		1 day chick		½ boiled egg		1 day chick
1330/1500/1600	7-12g insects	7-12g insects	7-12g insects	7-12g insects	7-12g insects	7-12g insects	7-12g insects
	Scatter feeding regime						
0800	20g vegetable	20g vegetable	20g vegetable	20g vegetable	20g vegetable	20g vegetable	20g vegetable
0930 to 1730 (20 times)	1g pellets	1g pellets	1g pellets	1g pellets	1g pellets	1g pellets	1g pellets
1300/1600	½ boiled egg		1 day chick		½ boiled egg		1 day chick
1500/1600	7-12g insects	7-12g insects	7-12g insects	7-12g insects	7-12g insects	7-12g insects	7-12g insects

Pelleted food: 3762 Insectivore extrudate, Granovit, Kaiseraugst, Switzerland (in % as fed: total ash 8.0, crude protein 23.0, crude fat 8.7, crude fibre 12.5)
Insects: crickets, coackroaches, grasshoppers. Feeding times of specific food items varied between days

walls. Thus, food was scattered over a radius of approximately six metres. The machine was easily visible for the meerkats and visitors and was set to distribute food 13 times (Walter Zoo, resulting in a total of 14 feedings, Table 1), 20 times (Zoo Zurich, 2 machines, resulting in a total of 23 feedings, Table 2) or 16 times (Parken Zoo, with a total of 17–18 feedings, Table 3) per day, so that each dispensing moment occurred during the active daytime period when the animals were already awake and could see and hear the machine dispensing food. The time interval between two machine feedings ranged between 5 and 90 minutes, set differently for each zoo according to zoo-specific influences such as additional feedings with visitors or the varying length of the day (depending on the season and latitude). Within a zoo, the same setting was programmed equally for all days. Food items that could not be dispensed by the scatter machine were cut into small pieces and distributed by hand over large areas in the enclosure.

At Zoo Zurich, an information sign including a QR code explained the research project.

Table 3. Feeding schedules (per animal) at Parken Zoo

Time	Monday	Tuesday	Wednesday	Thursday	Friday	Saturday	Sunday
	Lumped feeding regime						
1000	10g fruit 1 day chick 23g pellets	10g fruit 1 day chick 23g pellets	10g fruit 1 day chick 23g pellets	10g fruit 1 day chick 23g pellets	10g fruit 1 day chick 23g pellets	10g fruit 1 day chick 23g pellets	10g fruit 1 day chick 23g pellets
1200		15g Zophobas		15g Zophobas		15g Zophobas	
	Scatter feeding regime						
0830 to 1500 (16 times)	1.4g pellets	1.4g pellets	1.4g pellets	1.4 gpellets	1.4g pellets	1.4g pellets	1.4g pellets
1000	10g fruit 1 day chick	10g fruit 1 day chick	10g fruit 1 day chick	10g fruit 1 day chick	10g fruit 1 day chick	10g fruit 1 day chick	10g fruit 1 day chick
1200		15g Zophobas		15g Zophobas		15g Zophobas	

Pelleted food: 3762 Insectivore extrudate, Granovit, Kaiseraugst, Switzerland (in % as fed: total ash 8.0, crude protein 23.0, crude fat 8.7, crude fibre 12.5)

Table 4. Ethogram for behaviour recording of zoo meerkats *Suricata suricatta*

Behaviour (Abbreviation)	Definition	Zoos	Categories	Behavioural Groups
Food Guarding (FG)	Monopolizing food (Fig. 4B)	PZ, WZ, ZZ	Neg	Ag, A
Fighting (Fi)	Sudden rush towards each other with tail raised vertically, choppy rapid movements	PZ, WZ, ZZ	Neg	Ag, A
Stereotypic Behaviour (SB)	Repetition of the exact same movement without any reaction to external stimuli	PZ	Neg	A
Digging (Di)	Moving sand with both front paws simultaneously	PZ, WZ, ZZ	Neu	A
Drinking (Dr)	Drinking water	PZ, WZ, ZZ	Neu	A
Sitting (Si)	Not moving, sitting somewhere	PZ, WZ, ZZ	Neu	I
Lying Alone (LA)	Not moving, lying somewhere without contact/ interactions to others	PZ, WZ, ZZ	Neu	I
Standing Posture (SP)	Standing on rear legs and gazing over the enclosure	PZ, WZ, ZZ	Neu	I
Sun-Bathing (SB)	Standing/ lying in the sunlight for at least 5 seconds	PZ, WZ, ZZ	Neu	I
Locomotion (Lo)	Getting from one place to another by steady moving (either slowly or fast), with a stretched back	PZ, WZ, ZZ	Neu	A
Standing/Sitting by Entrance of Tunnel (ET)	Animal remains in front of the entrance to their sleeping tunnel, the back turned towards the entrance	PZ	Neu	I
Sleeping in Tunnel (ST)	The animal is in place in the tunnel without moving.	PZ	Neu	I
Eating Salad (ES)	Eating the salad or hay of the tortoises	WZ	Neu	FR, A
Alert (Al)	Animal under tension, focused on a specific matter, tail vertically raised, back bent in kyphosis, bouncing with the forelegs, chattering vocalisation	PZ, WZ, ZZ	Neu	A
Playing (Pl)	Engaged in play, alone or with others	PZ, WZ, ZZ	Pos	So, A
Grooming (Gr)	More than 5 seconds of grooming	PZ, WZ, ZZ	Pos	So, A
Lying Together (LT)	Being in physical contact without doing anything for at least 5 seconds	PZ, WZ, ZZ	Pos	So, I
Eating (Ea)	Being at one place and eating (Fig. 4C)	PZ, WZ, ZZ	Pos	FR, A
Nursing (Nu)	Breastfeeding - juvenile and alpha females	ZZ	Pos	So, A
Playing with Ball (PB)	Pushing ball around with head and front legs to reach food	WZ	Pos	A
Foraging (Fo)	Slowly walking with many changes in direction and stopping while the back is bent, collecting and ingesting food items (Fig. 4A)	PZ, WZ, ZZ	Pos	FR, A
Not visible (NV)	Animal not visible	PZ, WZ, ZZ	-	-

Zoos, PZ (Parken Zoo), WZ (Walter Zoo), ZZ (Zürich Zoo). Categories, Pos (Positive), Neu (Neutral), Neg (Negative). Behavioural groups, Ag (Angonistic), FR (Feeding related), So (Social), A (Active), I (Inactive).

Data collection

The behaviour of the animals was recorded by instantaneous sampling at a five-minute interval (Altmann 1974). For scan sampling, the animals were observed on site for about 30 seconds (to correctly identify the behaviour they were expressing in the instant) and the behaviour of all individuals visible at that time was recorded. The number of individuals not visible was later calculated by subtraction of all observed individuals from the total number of individuals. It was not possible at this time interval to identify individual animals; the data therefore represent the number of individuals observed performing a certain behaviour at that time. This method had been tested in pilot observations; in particular, tablet-based applications available to record behaviour electronically proved too slow for entering data for large groups (as entries had to be done for each individual).

A single observer was situated outside the enclosure in the visitor area in order not to influence the animals. Whether observer presence had an effect on the animals was not assessed, but the same observer presence was kept constant during all A-B-A-B-A observation periods. The behaviour of the meerkats was recorded depending on the time the animals emerged from and retreated to their dens in the respective zoos, ideally from sunrise to sunset in accordance with the opening hours of the respective zoo.

The ethogram used for the observations was based on behaviours already described in meerkats (Greene 2016; Mausbach 2017; Scott 2014). Of particular interest were the behaviours of foraging (Figure 4A), food monopolisation (Figure 4B) and stationary feeding (Figure 4C). Additions to the behaviours used previously in ethograms were made based on the observations in this study (Table 4). Behaviours were additionally classified into qualitative categories (positive, neutral, negative or not visible) and grouped into general divisions (agonistic, feeding related, social). Likewise, each behaviour was considered active or inactive.

http://doi/org/10.19227/jzar.v12i3.828

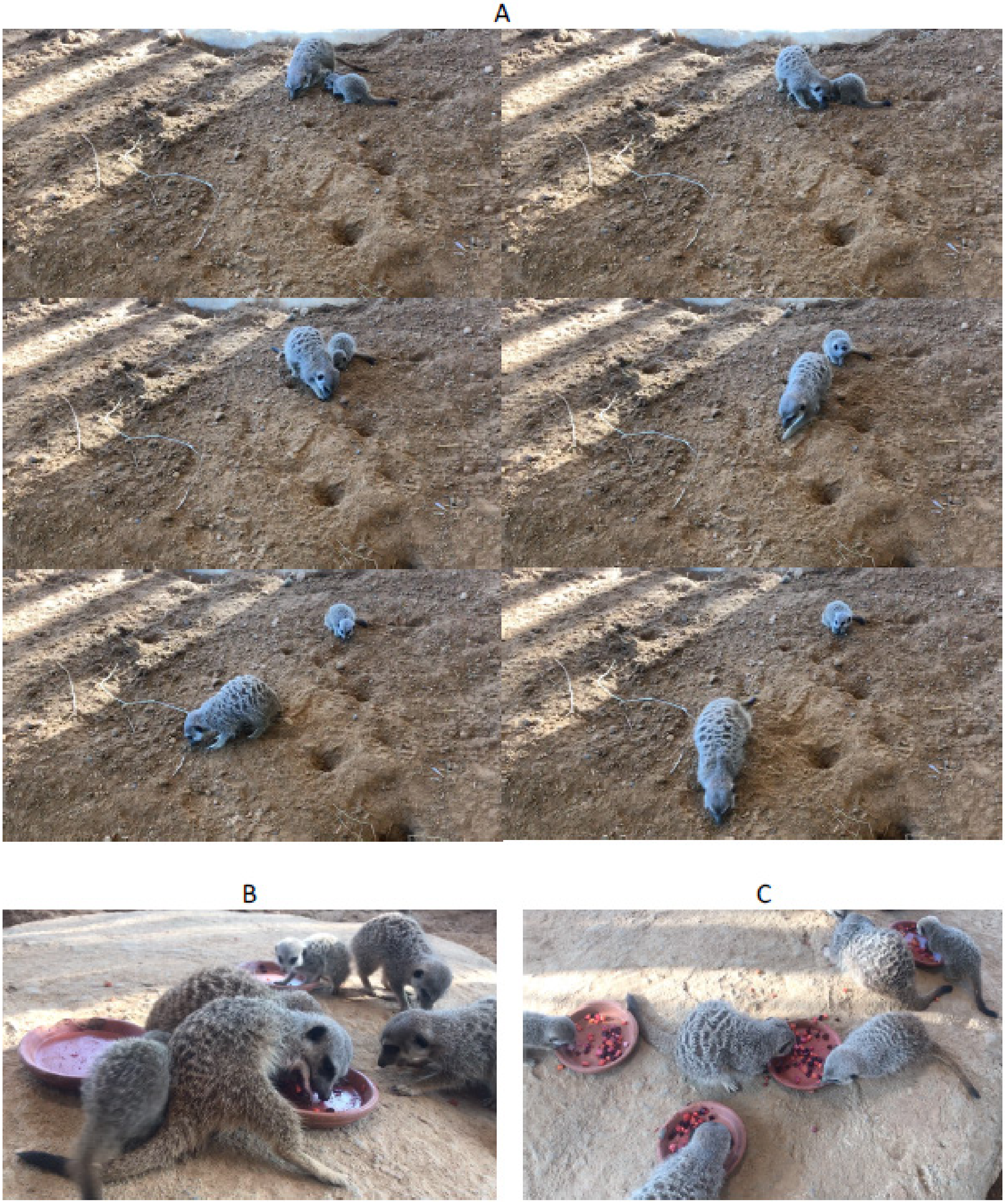

Figure 4. Different behaviours in zoo meerkats *Suricata suricatta*: A foraging behaviour, slowly walking with many changes in direction and stopping while the back is bent, collecting and ingesting food items; B food guarding, monopolising food, using the whole body to block access of conspecifics; C eating, being at one place and eating, stationary food intake

Data analysis

The data consisted of counts of the number of animals observed performing the different behaviours (and 'not visible') at each 5-minute observation interval. These counts were then expressed as the percentage of animals (of the total number of animals present in the enclosure) engaged in a specific behaviour at that observation interval. These original data were aggregated into averages representing longer time periods: an average per hour, an average per day and an average per four-day observation period.

Because data could not be recorded on an individual basis, the whole group was the sampling unit at each zoo. To avoid pseudo-replication (Kuhar 2006), it was necessary to account for the fact that this sampling unit was measured repeatedly; therefore, mixed

Table 5. Results of statistical comparisons of treatments (lumped feeding versus scatter feeding) using mixed effects linear models with 'Zoo' as a random effect to account for repeated measures, based on averages of percentage of individuals observed performing the behaviour per study period (n=15 observations, five periods per each of three zoos; degrees of freedom=11) of original data, except for 'Food guarding' for which ranked data had to be used. A positive t value indicates more frequent behaviour under the scatter feeding treatment; see also Figure 7. For a definition of behaviours, see the ethogram Table 4

	Treatment		Zoo
Behaviour	t	P	P
Active	5.76	<0.001	0.004
Not visible	-1.95	0.077	<0.001
Foraging	15.69	<0.001	0.127
Eating	-9.08	<0.001	1.000
Feeding	12.90	<0.001	0.087
Food guarding°	-3.82	0.003	0.010
Social	-0.30	0.767	0.049

°ranked data

effects linear models were used in R (R Core Team 2023) using the lmerTest package (Kuznetsova et al. 2017) with a random factor that accounted for the repeated measurements. To assess model adequacy, the normal distribution of the residuals was assessed using the Shapiro-Wilk test. If the residuals were not normally distributed, the model was repeated with ranked data in a non-parametric approach.

Due to the structure of the data, several alternative models were used to address the question of whether the treatment (lumped versus scatter-feeding) had a significant effect on the behaviour budget. This paper presents results comparing the averages of the five study periods across zoos (n=15 observations) in an approach that used zoo as the random factor. Whether the random factor zoo had a significant effect was assessed using the likelihood ratio score comparing the likelihood of the model with the random factor to one without it. Additionally (documented in Supplementary Information 2), averages per day (n=60 observations) were compared in an approach that used period nested in zoo as the random factor and the averages per hour (n=560 observations) in an approach that used day nested in period nested in zoo as the random factor. The effect of treatment within each zoo was also assessed individually. For more details on these latter approaches, which all yielded similar results to those reported in the main text, see Supplementary Information 2.

Results

At Walter Zoo and Zoo Zurich, the animals adapted rapidly to the new feeding regime. Over a single day, the meerkats adjusted to foraging for the scattered diet items. After only a few days, none of the animals displayed fear of the scatter machine but appeared to associate feeding opportunities with its activation. At Parken Zoo, by contrast it took the animals two weeks to adapt. The animals were introduced to the scatter-feeding regime more gradually, by first habituating them to feed not only from a bowl but from the ground, through a stepwise enlargement of the feeding area and finally by adapting them to the scatter machine.

Behaviours that were not recorded at each zoo included stereotyping (only recorded at Parken Zoo), behaviours related to the tunnel entrance at Parken Zoo, nursing at Zoo Zurich and playing with enrichment balls as well as eating salad fed to the tortoises at Walter Zoo.

At all zoos, behaviours were generally spread evenly across the day with no distinct peaks of a specific activity (Figure 5). While there was a significant random effect of the zoos, indicating differences in the activity budgets across the three zoos (Table 5), there were also significant differences in the activity budget between the feeding periods across all zoos (Table 5, Figure 6). During scatter-feeding, meerkats were significantly more active, foraged more frequently, showed less food monopolising behaviour ($P<0.05$) and tended to be more visible ($P=0.077$). During lumped feeding, eating (defined as ingestion while stationary) was more frequent ($P<0.05$). No systematic difference was found for social behaviour ($P=0.767$). In the zoo where stereotypy was observed (on the order of 40–165 min per day), the different feeding regimes had no effect on the frequency of this behaviour (Supplementary Information 2).

A final qualitative observation was made with respect to the group behaviour during feeding: for all colonies, all animals would generally eat as soon as they were fed in the lumped feeding sessions; by contrast, during scatter-feeding, individual animals would stop feeding and take turns at guarding while the rest of the group was foraging (Figure 7A, B). Animals abstaining from foraging and guarding their group were seen in more than half of the feedings during scatter-feeding. This detail was noticed when observing the animals at Zoo Zurich and could subsequently be confirmed at Parken Zoo. No statement can be made with respect to Walter Zoo where the first experiment was performed and this behaviour was not observed, but also not paid attention to and therefore might have been overlooked.

Discussion

As expected, the scatter feeder significantly increased the time the meerkats spent foraging in all three facilities. In combination with a dry food of sufficiently small particle size, the use of the scatter machine proved feasible for the objective. In two of the three facilities, a natural behaviour (sentinel guarding while the group is foraging directly when and after being fed) was elicited during scatter-feeding that was not observed during lumped feeding. Before discussing these findings in more detail, some limitations of the present study and of the specific scatter machine are outlined.

The importance of recognising technical faults should not be underestimated. In the case of automated feedings, technical failures would have important consequences for the welfare of the animals. During the study, the machine was monitored constantly by the first author. However, constant monitoring is not feasible under normal zoo routines and therefore it is important to find a way for daily control. This could be achieved for example by hanging the machine on a spring scale allowing keepers to assess whether the daily ration has effectively been fed to the animals. The feeder used in the present study is only suitable for dry pellets or extrudates; additional feeding of insects/vegetables provides the animals with some diversity and allows the keepers to see and evaluate the animals every day. Note however, that the value of diversity may be readily overrated in its effect on nutrient intake or animal welfare and should not be considered a priority over supply with a complete food (Dobbs et al. 2020). Daily inspection of the animals cannot be replaced by the use of automated feeding machines and is mandatory. In Sweden, for example, it is required by law that "animals shall be kept in such a way that they can be easily supervised. Supervision shall be carried out at least

http://doi/org/10.19227/jzar.v12i3.828

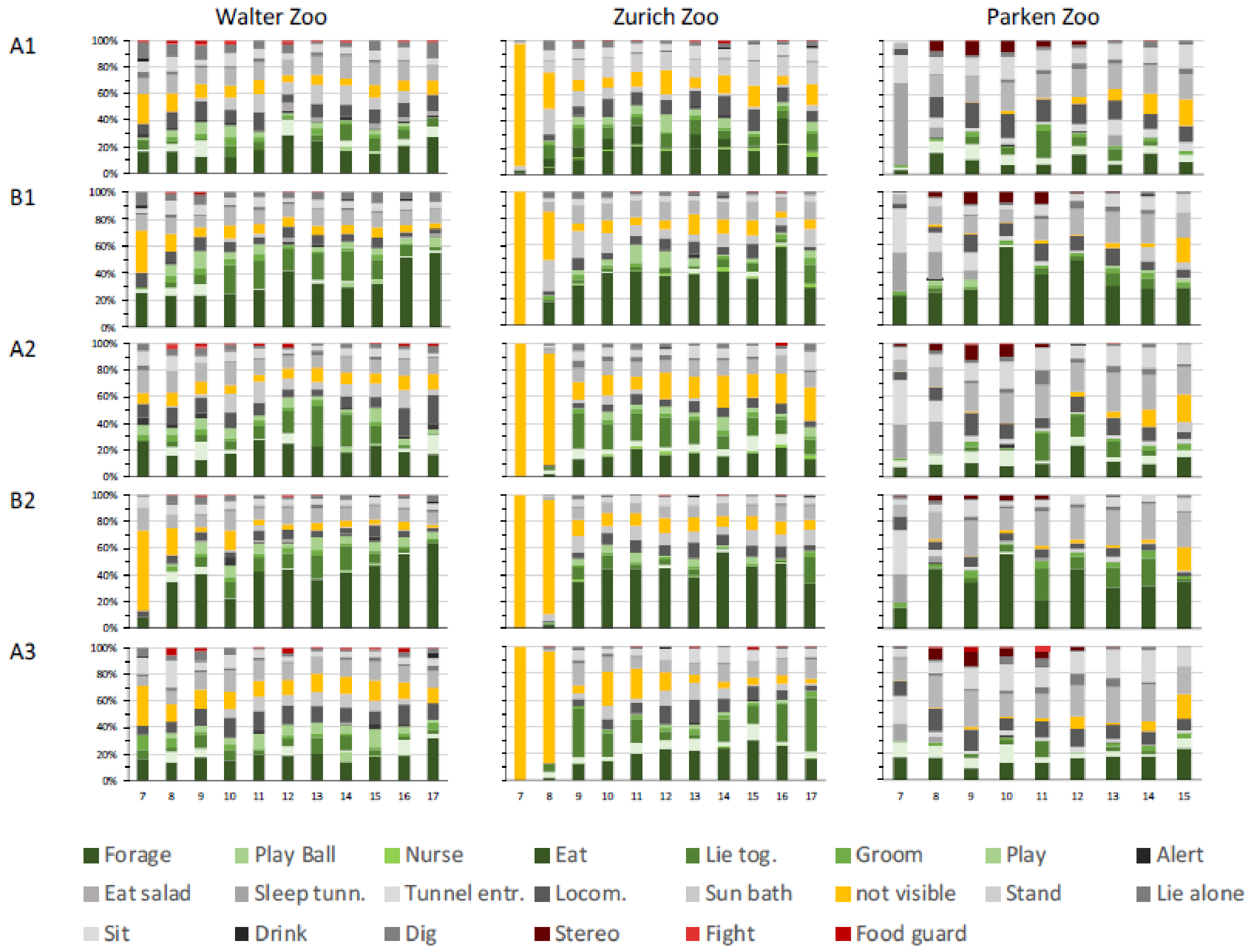

Figure 5. Proportion of different activities in % of all observations by hourly interval of the active day for meerkats *Suricata suricatta* at three different zoos under two feeding regimes (A: lumped feeding; B: scatter feeding) applied in an A-B-A-B-A scheme for a total of five weeks

once a day" (SBA 2019). In the authors' experience, the scatter feeder used here can be easily cleaned and represents no hygiene risk (see Supplementary Information 2).

During this study, meerkats appeared to adapt to the feeding regimes comparatively easily with hardly any notable transition at two of the three zoos. Even the group of older animals, which had never experienced scatter-feeding or feeding from anything but a food bowl for years, adjusted to the new feeding method.

The scatter-feeding regime achieved a relevant impact on foraging behaviour. By scattering food between 14 and 23 times per day, an increase in daily foraging behaviour could be achieved from 16% during lumped feeding to 36% during scatter-feeding days (Figure 8). To the authors' knowledge, the only published activity budget of free-ranging meerkats that quantifies foraging behaviour is the thesis of Habicher (2009). In that thesis, an overall activity budget for three meerkat groups indicates foraging times of 37% of the observed time (in a total of 119,160 scans during 228 hours between 0600 and 1900) (Habicher 2009). Thus, automated scatter-feeding increased the foraging behaviour of the meerkats in the three zoos included in this study to frequencies observed in the natural habitat (Figure 8). Here, a word of caution is required following e.g. the considerations of Browning (2020). That a behaviour or an activity budget at the zoo is different from that in a natural habitat is in itself not necessarily an indication of reduced welfare. Not all behaviours expressed in natural habitats are indicative of positive welfare, and there are also important examples of behaviours expressed in zoos that do not occur in natural habitats yet are most parsimoniously interpreted as indicators of high welfare (e.g. De Rouck et al. 2005; van Schaik et al. 2016). Rather, the specific behaviours have to be scrutinised individually. In the case of the meerkats exposed to scatter-feeding, the increase in foraging time that made the zoo activity budget more similar to that of free-ranging conspecifics can be expected to have several—putatively positive—consequences.

Wild female meerkats have a predicted energy intake of 315–383 kcal ME/day (or 1,318–1,602 kJ) while obese meerkats in zoos are suggested to need only around 114 kcal ME/day (or 477 kJ) to maintain their body mass—less than half that of their

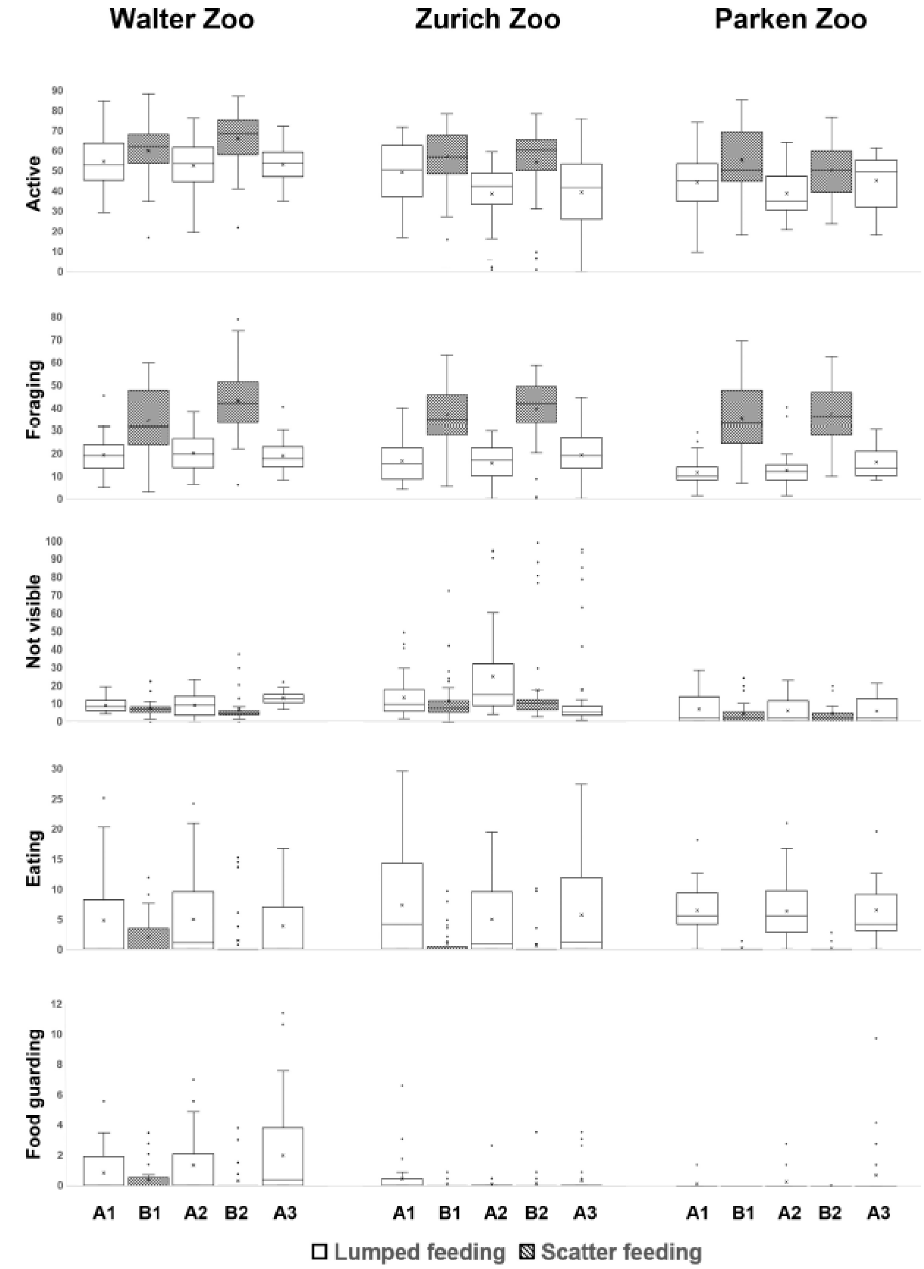

Figure 6. Comparison of periods when lumped (A1-A3) or scatter feeding (B1, B2) took place shown as boxplots for the behaviour categories active, foraging, not visible, eating and food guarding. Horizontal lines within the box correspond to the median, crosses to the mean. The boxes indicate the upper and lower quartile, whiskers represent the 1.5 x interquartile range, and individual dots represent outliers outside of that range. The y-axis corresponds to the frequency of the behaviour in percent

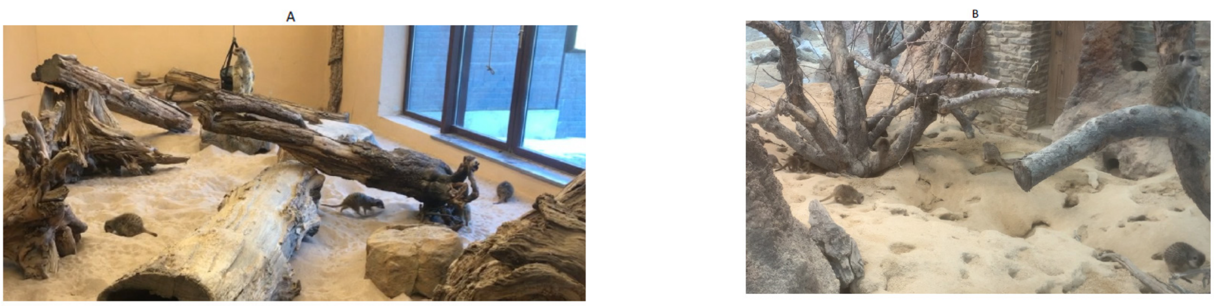

Figure 7. Guarding behaviour by an individual zoo meerkat *Suricata suricatta* while conspecifics are foraging after a scatter-feeding event: A Parken Zoo; B Zoo Zurich

http://doi/org/10.19227/jzar.v12i3.828

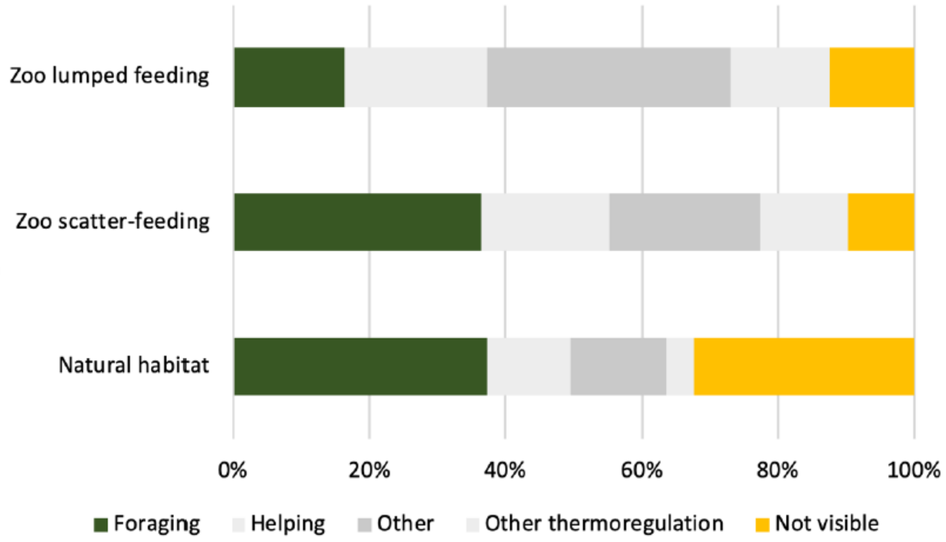

Figure 8. Overall daytime activity budgets of meerkats *Suricata suricatta* under two different feeding regimes: lumped feeding (A) versus scatter feeding (B) summarised out of a five-week A-B-A-B-A scheme in the three different zoos; this is compared to the overall daytime activity budget of three meerkat groups free-ranging in a natural habitat from Habicher (2009). Zoo data are aggregated to correspond to the categories of the study in free-ranging animals. 'Helping' includes guarding, digging, babysitting and pup feeding; 'Other' includes lying, grooming, sitting, standing, locomotion, eating, playing and agonistic behaviour; 'Other thermoregulation' includes sunbathing, contact lying and huddling

wild relatives (Gutzmann et al. 2009). Scatter-feeding can increase active behaviour significantly compared with the activity shown during lumped feeding. Activating the meerkats with a frequent scatter-feeding regime could therefore help counteract obesity—a common, known husbandry issue in zoo-housed meerkats (AZA Small Carnivore TAG 2011).

Foraging can be seen both as an additional positive enrichment and a release for energy, and decreases the animals' exposure to negative stress (Morgan and Tromborg 2007) and reduces the opportunity for undesirable behaviours. In the current study, a strong decrease in food monopolisation behaviour was observed; the behaviour was practically no longer present during the scatter-feeding regime (Figure 6). Scatter feeding has been documented to have a variety of positive effects across species. Red river hogs spent more time foraging and less time immobile with scatter-feeding (Farmer et al. 2006) and more time in public view when attracted by an automated scatter-feeder (Moore and Powell 2012). Malayan sun bears *Helarctos malayanus* spent more time foraging when scatter-feeding was used (Schneider et al. 2014). Grizzly bears showed an increase in active behaviour and a decrease in repetitive behaviours while an automatic scatter feeder was used (Andrews and Ha 2014). Stereotypic behaviour could be reduced through scatter-feeding in red pandas *Ailurus fulgens fulgens* (Khan 2022). In broilers *Gallus gallus domesticus*, reduced pecking was shown under scatter-feeding (de Jong et al. 2005), facilitating a dramatic increase in animal welfare. Furthermore, in a comparison between an enrichment device and scatter-feeding, the latter led to a significantly higher frequency of almost all analysed behaviours associated with activity in an insectivorous lizard *Plica plica* (Januszczak et al. 2016).

The more active behaviour during scatter-feeding sessions compared with the lumped feeding session likely increases the attractiveness of the animals for visitors. Although this was not quantified, visitors repeatedly showed curiosity about the feeding machine, speculating about its purpose—until that became evident. When observing a scatter distribution by the machine, many visitors made links to the foraging meerkats on their own initiative, which showed that visitors are willing to analyse and discuss what is happening in zoo enclosures. When it comes to seeing the zoo not just as a place for relaxation but also as a place where knowledge is exchanged, the scatter machine offers a welcome introduction to the conversation with visitors and makes it possible to address topics that are important regarding animal husbandry and welfare.

In addition to making the activity budgets of the animals more similar to that of free-ranging conspecifics in terms of time spent foraging, the many individual scatter-feeding events also elicited the sentinel behaviour for which meerkats are well known (Clutton-Brock et al. 1999; Manser 1999; Rauber and Manser 2021) in two of the three facilities during feeding. In fact, sentinel behaviour was to the authors' knowledge first described in zoo meerkats (Moran 1984) and is often observed in zoos (I. Bähler and M. Clauss personal observation). However, to the authors' knowledge it has not been reported in the context of feeding. During few lumped feeding events in a traditional feeding regime, a sentinel individual would miss out on feeding opportunities. It may only be at the high frequency of scatter-feeding achieved in the present study that animals can afford to act as sentinels. It was shown previously that another aspect of the meerkat sentinel system is still present in zoo meerkats, namely the response to alarm calls of different quality (Schneider et al. 2021). Achieving this natural behaviour may additionally increase the display value of meerkats. Similarly, behaviours previously not observed in zoos were triggered with special feeding methods in other species. Macaques *Macaca* spp. subjected to scatter-feeding filled their cheek pouches with food and climbed to a high location to eat—a species-specific behaviour that had never been observed in the studied subjects before (Cannon et al. 2016). Giant otters *Pteronura brasiliensis* exposed to a slow-release feeding method that provided food well into the night were observed to call sleeping family members to the food and specifically incite their young to feed, a behaviour previously only reported in the wild (Friedmann et al. 2023). Creating opportunities for zoo animals to acquire food outside of a few fixed times per day may elicit previously unobserved behaviours.

Environmental enrichment (EE) strategies have become part of standard zoo husbandry to maintain zoo-housed animals in a good physical and mental condition. EE is either defined as a concept of environmental changes benefiting its inhabitants or as a process for improving environments within the context of the inhabitants' natural history and behavioural biology (Young 2003). It is often expected that EE should enhance natural behaviours in zoo animals (McPhee and Carlstead 2010). This is even required by law in the Swiss Federal Ordinance on Animal Welfare (FSVO 2008) which states: "Feeding must simulate the species-typical characteristics of food intake (spatially and temporally varying feed supply, feed procurement, feed processing and duration of feed intake)". As early as 1997, Young (1997) wrote: "if zoos are to be successful,…, in their concern for animal welfare, they must give serious consideration to the interface between diet and behavioural processes". Nowadays, decades later, though many zoos are striving to improve traditional feeding practices, EE methods are often not used routinely (Kleinlugtenbelt et al. 2023). Single bowl feeding is still a daily reality for different species kept in zoos (I. Bähler personal observation) and for animals kept as pets (Heys et al. 2024). The gap between current knowledge and recent findings with what is effectively applied in everyday zoo management needs to be better understood, hurdles for putting recommendations into practice need to be identified and strategies need to be developed about how to overcome those hurdles for effective implementation of feeding methods that take behavioural management and hence animal welfare into account (Fens and Clauss 2024).

Automated scatter-feeding could be an effective approach to make multiple daily feedings less dependent on the keepers' schedule and allow keepers to allocate resources to other aspects such as observation and training, increasing animal welfare and benefiting both the animals and their keepers. Increased animal welfare was shown to increase zookeeper job satisfaction (Riggio et al. 2020). Keepers are one of the important links in the chain between the latest knowledge and what is actually found in zoo enclosures. Automated feeders provide relief in the daily routine, thus providing an ideal basis for an independent, constant and efficient feeding and therefore show themselves as a valuable tool for good animal welfare.

Acknowledgments

The authors are very grateful to the animal keeper teams of Parken Zoo, Walter Zoo and Zoo Zurich for the support of this study, in particular C. Brandenberger, J. Gustafsson, K. Hug, J. Johnsson, A. Leuenberger and P. Lundgren. The authors thank two anonymous reviewers for their valuable suggestions.

References

Altmann J. (1974) Observational study of behavior: Sampling methods. *Behaviour* 49(3–4): 227–266. doi:10.1163/156853974X00534

Amici F., Mimó M.C., von Borell C., Bueno-Guerra N. (2017) Meerkats (*Suricata suricatta*) fail to prosocially donate food in an experimental set-up. *Animal Cognition* 20:1059–1066. doi:10.1007/s10071-017-1122-6

Andrews N.L.P., Ha J.C. (2014) The effects of automated scatter feeders on captive grizzly bear activity budgets. *Journal of Applied Animal Welfare Science* 17(2): 148–156. doi:10.1080/10888705.2013.856767

AZA Small Carnivore TAG (2011) *Mongoose, Meerkat, & Fossa (Herpestidae/ Eupleridae) Care Manual*. Silver Spring, Maryland: Association of Zoos and Aquariums.

Browning H. (2020) The natural behavior debate: Two conceptions of animal welfare. *Journal of Applied Animal Welfare Science* 23(3): 325–337. doi:10.1080/10888705.2019.1672552

Cannon T.H., Heistermann M., Hankison S.J., Hockings K.J., McLennan M.R. (2016) Tailored enrichment strategies and stereotypic behavior in captive individually housed macaques (*Macaca* spp.). *Journal of Applied Animal Welfare Science* 19(2): 171–182. doi:10.1080/10888705.2015.1126786

Charmoy K., Sullivan T., Miller L.J. (2015) Impact of different forms of environmental enrichment on foraging and activity levels in gorillas (*Gorilla gorilla gorilla*). *Animal Behavior and Cognition* 2(3): 233–240. doi:10.12966/abc.08.03.2015

Clutton-Brock T.H., O'Riain M.J., Brotherton P.N.M., Gaynor D., Kansky R., Griffin A.S., Manser M. (1999) Selfish sentinels in cooperative mammals. *Science* 284(5420): 1640–1644. doi:10.1126/science.284.5420.1640

Cummings D., Brown J.L., Rodden M.D., Songsasen N. (2007) Behavioral and physiologic responses to environmental enrichment in the maned wolf (*Chrysocyon brachyurus*). *Zoo Biology* 26(5): 331–343.

de Jong I.C., Fillerup M., Blokhuis H.J. (2005) Effect of scattered feeding and feeding twice a day during rearing on indicators of hunger and frustration in broiler breeders. *Applied Animal Behaviour Science* 92(1–2): 61–76. doi:10.1016/j.applanim.2004.10.022

De Rouck M., Kitchener A.C., Law G., Nelissen M. (2005) A comparative study of the influence of social housing conditions on the behaviour of captive tigers (*Panthera tigris*). *Animal Welfare* 14(3): 229–238. doi:10.1017/S0962728600029390

Dobbs P., Liptovszky M., Moittie S. (2020) Dietary management of hypercholesterolemia in a bachelor group of zoo-housed Slender-tailed meerkats (*Suricata suricatta*). *Journal of Zoo and Aquarium Research* 8(4): 294–296. doi:10.19227/jzar.v8i4.535

Doolan S.P., MacDonald D.W. (1996) Diet and foraging behaviour of group-living meerkats, *Suricata suricatta*, in the southern Kalahari. *Journal of Zoology* 239(4): 697–716. doi:10.1111/j.1469-7998.1996.tb05472.x

Farmer H., Dayrell E., Pullen K. (2006) Encouraging enclosure use in red river hogs using scatter feeding. Shape of Enrichment 15: 11–15.

Fens A., Clauss M. (2024) Nutrition as an integral part of behavioural management of zoo animals. *Journal of Zoo and Aquarium Research* (in press).

Fischbacher M., Schmid H. (1999) Feeding enrichment and stereotypic behavior in spectacled bears. *Zoo Biology* 18(5): 363–371. doi:10.1002/(SICI)1098-2361(1999)18:5%3C363::AID-ZOO1%3E3.0.CO;2-H

Friedmann M., Burkevica A., Lagerström L., Gustafsson J., Johnsson J., Lundgren P., Clauss M. (2023) Activity budget and behaviour of giant otters Pteronura brasiliensis at Parken Zoo, Eskilstuna, Sweden. *Journal of Zoo and Aquarium Research* 11(4): 356–365.

FSVO (2008) *Swiss Federal Ordinance on Animal Welfare.* Bern, Switzerland: Federal Food Safety and Veterinary Office.

Greene L.K., Goncalves I.B., Fenkes M., Wisse J.H., Drewe J.A., Manser M.B., Clutton-Brock T., Drea, C.M. (2016) Beyond aggression: Androgen-receptor blockade modulates social interaction in wild meerkats. *Hormones and Behavior* 78: 95–106.

Gutzmann L.D., Hill H.K., Koutsos E.A. (2009) Biochemical and physiological observations in meerkats (*Suricata suricatta*) at two zoos during a dietary transition to a diet designed for insectivores. *Zoo Biology* 28(4): 307–318. doi:10.1002/zoo.20230

Habicher A. (2009) Behavioural Cost Minimisation and Minimal Invasive Blood-Sampling in Meerkats (*S. suricatta*, Herpestidae). Cologne, Germany: Universität zu Köln, Doctoral thesis.

Heys M., Lloyd I., Westgarth C. (2024) 'Bowls are boring': Investigating enrichment feeding for pet dogs and the perceived benefits and challenges. *Veterinary Record* 194(4): e3169. doi:10.1002/vetr.3169

Jadali N., Zhang M.J., Schulz A.K., Meyerchick J., Hu D.L. (2023) ForageFeeder: A low-cost open source feeder for randomly distributing food. *HardwareX* 14: e00405. doi:10.1016/j.ohx.2023.e00405

Januszczak I.S., Bryant Z., Tapley B., Gill I., Harding L., Michaels C.J. (2016) Is behavioural enrichment always a success? Comparing food presentation strategies in an insectivorous lizard (*Plica plica*). *Applied Animal Behaviour Science* 183: 95–103. doi:10.1016/j.applanim.2016.07.009

Jenny S., Schmid H. (2002) Effect of feeding boxes on the behavior of stereotyping Amur tigers (*Panthera tigris altaica*) in the Zurich Zoo, Zurich, Switzerland. *Zoo Biology* 21(6): 573–584. doi:10.1002/zoo.10061

Jordan N.R., Cherry M.I., Manser M.B. (2007) Latrine distribution and patterns of use by wild meerkats: Implications for territory and mate defence. *Animal Behaviour* 73(4): 613–622. doi:10.1016/j.anbehav.2006.06.010

Khan A.S. (2022) The influence of food-based enrichment on the behaviour of captive red pandas Ailurus fulgens fulgens. ResearchSquare preprint. doi:10.21203/rs.3.rs-2032386/v1

Kleinlugtenbelt C.L.M., Burkevica A., Clauss M. (2023) Large carnivore feeding in European zoos. *Der Zoolgische Garten* 91: 9–39. doi:10.53188/zg0012

Krebs B.L., Watters J.V. (2017) Simple but temporally unpredictable puzzles are cognitive enrichment. *Animal Behavior and Cognition* 4(1): 119–134. doi:10.12966/abc.09.02.2017

Kuhar C.W. (2006) In the deep end: Pooling data and other statistical challenges of zoo and aquarium research. *Zoo Biology* 25(4): 339–352. doi:10.1002/zoo.20089

Kuznetsova A., Brockhoff P.B., Christensen R.H.B. (2017) lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software* 82(13): 1–26.

Manser M.B. (1999) Response of foraging group members to sentinel calls in suricates, *Suricata suricatta. Proceedings of the Royal Society B* 266(1423): 1013–1019. doi:10.1098/rspb.1999.0737

Maple T.L., Perdue B.M. (2013) *Zoo Animal Welfare*. Berlin, Germany: Springer.

Mausbach J., Braga Goncalves I., Heistermann M., Ganswindt A., Manser M.B. (2017) Meerkat close calling patterns are linked to sex, social category, season and wind, but not fecal glucocorticoid metabolite concentrations. *PloS One* 12, e0175371.

McPhee M.E., Carlstead K. (2010) The importance of maintaining natural behaviors in captive mammals. In: Kleiman D.G., Thompson K.V., Baer C.K. (eds.). *Wild Mammals in Captivity: Principles and Techniques for Zoo Management Vol. 2*. Chicago, Illinois: Chicago University Press, 303–313.

Moore B., Powell D. (2012) Use of automatic feeders for red river hogs. *Shape of Enrichment* 21: 10–11.

Moran G. (1984) Vigilance behaviour and alarm calls in a captive group of meerkats, *Suricata suricatta. Zeitschrift für Tierpsychologie* 65(3): 228–240. doi:10.1111/j.1439-0310.1984.tb00101.x

Morgan K.N., Tromborg C.T. (2007) Sources of stress in captivity. *Applied Animal Behaviour Science* 102(3–4): 262–302. doi:10.1016/j.applanim.2006.05.032

Podturkin A.A., Papaeva N. (2020) Development of an environmental enrichment programme: Case study of white bengal tiger (*Panthera tigris bengalensis*) and jaguar (*Panthera onca*) at Moscow Zoo. *Journal of Zoo and Aquarium Research* 8(2): 139–145. doi:10.19227/jzar.v8i2.393

R Core Team (2023) *R: A Language and Environment for Statistical Computing.* Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org

Rad F., Kurt G., Bozaoğlu A.S. (2004) Effects of spatially localized and dispersed patterns of feed distribution on the growth, size dispersion and feed conversion ratio of the African Catfish (*Clarias gariepinus*). *Turkish Journal of Veterinary and Animal Sciences* 28(5): 851–856.

Rauber R., Manser M.B. (2021) Effect of group size and experience on the ontogeny of sentinel calling behaviour in meerkats. *Animal Behaviour* 171: 129–138. doi:10.1016/j.anbehav.2020.11.014

Riber A.B., van De Weerd H.A., de Jong I.C., Steenfeldt S. (2018) Review of environmental enrichment for broiler chickens. *Poultry Science* 97(2): 378–396. doi:10.3382/ps/pex344

Riber A.B. (2006) Habitat use and behaviour of European hedgehog *Erinaceus europaeus* in a Danish rural area. *Acta Theriologica* 51: 363–371. doi:10.1007/BF03195183

Riggio G., Pirrone F., Lunghini E., Gazzano A., Mariti C. (2020) Zookeepers' perception of zoo canid welfare and its effect on job satisfaction, worldwide. *Animals* 10(5): 916. doi:10.3390/ani10050916

Riley L.M., Rose P.E. (2020) Concepts, applications, uses and evaluation of environmental enrichment: Perceptions of zoo professionals. *Journal of Zoo and Aquarium Research* 8(1): 18–28. doi:10.19227/jzar.v8i1.384

SBA (2019) N*ational Agricultural Legislation on Animal Husbandry in Zoos.* Jönköping, Sweden: Swedish Board of Agriculture.

Schneider M., Nogge G., Kolter L. (2014) Implementing unpredictability in feeding enrichment for Malayan sun bears (*Helarctos malayanus*). *Zoo Biology* 33(1): 54–62. doi:10.1002/zoo.21112

Schneider S., Goettlich S., Diercks C., Dierkes P.W. (2021) Discrimination of acoustic stimuli and maintenance of graded alarm call structure in captive meerkats. *Animals* 11(11): 3064. doi:10.3390/ani11113064

Scott K. (2014) *Behaviour and endocrinology of meerkats in zoos*. PhD Thesis, University of Exeter (United Kingdom).

Shepherdson D., Brownback T., James A. (1989) A mealworm dispenser for the Slender-tailed meerkat *Suricata suricatta* at London Zoo. *International Zoo Yearbook* 28(1): 268–271. doi:10.1111/j.1748-1090.1989.tb03298.x

Tatalović M. (2012) First quantitative description of sentinel posts in wild meerkats. *Natura Croatica* 21(2): 493–496.

Tomczyk K., Zieliński D. (2021) The use of environmental enrichments on the meerkats' run (*Suricata suricatta*) in zoo conditions to eliminate aggressive behaviors. *Nauki Przyrodnicze i Medyczne* 32(2): 37–44.

van Schaik C.P., Burkart J., Damerius L., Forss S.I.F., Koops K., van Noordwijk M.A., Schuppli C. (2016) The reluctant innovator: Orangutans and the phylogeny of creativity. *Philosophical Transactions of the Royal Society B* 371(1690): 20150183. doi:10.1098/rstb.2015.0183

Veasey J.S., Waran N.K., Young R.J. (1996) On comparing the behaviour of zoo housed animals with wild conspecifics as a welfare indicator. *Animal Welfare* 5(1): 13–24. doi:10.1017/S0962728600018297

Waters S., Smeeton C. (2002) *An Update on Guzoo Animal Farm*. Toronto, Canada: World Society for the Protection of Animals.

Watters J.V., Miller J.T., Sullivan T.J. (2011) Note on optimizing environmental enrichment: A study of fennec fox and zoo guests. *Zoo Biology* 30(6): 647–654. doi:10.1002/zoo.20365

Young R.J. (1997) The importance of food presentation for animal welfare and conservation. *Proceedings of the Nutrition Society* 56(3): 1095–1104. doi:10.1079/PNS19970113

Young R.J. (2003) *Environmental Enrichment for Captive Animals*. Oxford, UK: Blackwell Science.