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Review article

Nutrition as an integral part of behavioural management of zoo animals

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Abstract

Provision of optimal diets for wild animals in captivity can have beneficial effects on health, reproductive performance and welfare. Zoo animal nutrition has made significant advances over the past decades; however adequate diet provision in zoological institutions remains challenging. This paper proposes a schematic history of developments in zoo animal nutrition in four steps, from finding diet items an animal will readily accept to secure its immediate survival (step 1), to supplementing these diet items with essential nutrients like minerals and vitamins (step 2), replacing convenient diet items from step 1 with items that are nutritionally and structurally more adequate for the species (the culturally challenging step 3) and providing the step 3 diet in species-appropriate ways to achieve behavioural management goals (step 4). Within this model, general rules of feeding behaviour are considered, emphasising the importance of promoting natural behaviours through adequate feeding management rather than simply preventing nutritional imbalances. By providing several short case studies, knowledge of feeding behaviour and activity budgets of several mammalian species is used as a guideline for adequate feeding management. Since the developments in feeding regimes described often cannot be made in synchrony across species or across zoos, it remains challenging for zoos to progress towards the final step. Therefore, this paper aims to inspire zoos by providing suggestions for moving towards integral feeding regimes for animals in their care and to assess where they stand in the four-step process with respect to certain animal groups. In conclusion, active application of knowledge of both dietary requirements and natural feeding ecology are essential for improving dietary feeding management in zoos and hence animal welfare.

Introduction

The provision of an appropriate diet is a crucial element of animal husbandry, including of zoo animal populations. Nutrition has distinct effects on animal health, reproductive performance and welfare. When considering zoo animal nutrition, the focus of attention may vary among these aspects, or logistical aspects of availability, hygiene or costs. Although there have been considerable developments in the science of zoo animal nutrition and dietary management, providing a nutritionally balanced diet to a broad array of taxonomic groups remains challenging. This review stresses the role nutrition plays in the behavioural management of wild animals in captivity. First, a summative overview of historical developments in zoo animal nutrition is given. Then some general rules on feeding behaviour are outlined. Several short examples illustrate how nutrition influences behaviour in human care. This paper does not aim to provide a comprehensive literature review but gives citations as examples. For brevity, the focus and examples are drawn from this taxon. Nevertheless, similar principles will apply to other taxa.

A brief history of zoo animal nutrition

The general history of zoo animal nutrition and the history of developing a feeding regime for a particular species can be summarised in a four-step model. This model may not be universal and comprehensive. While the sequence appears relatively constant, it may be that while a majority of zoos are already in step 3 for a group of species, they are still in step 2 for another set of species; and some other zoos might still be in steps 2 and 1, respectively. Developments are not made in synchrony across species, across zoos or even across species and sections within an individual zoo. Evaluating to what extent anecdotal or scientific communication affects progress from one step to another within or between zoos is beyond this review. Zoos have been sharing diet information for a very long time, for example in the 1966 issue of the International Zoo Yearbook (Hediger 1966; Ratcliffe 1966; Wackernagel 1966) or the 1977 CRC handbook series (Rechcigl 1977a, b) and in numerous individual publications and husbandry guidelines. It is expected that a recently founded zoo or a zoo that begins keeping a new species nowadays would begin the feeding management process at step 3 or 4 rather than step 2. However, the authors have encountered dietary recommendations and diets actually fed that do not correspond to current nutritional knowledge.

Step 1: Immediate survival

In the initial stages of zoo husbandry of a species, it is crucial to find a food that the animals will actually ingest, hence allowing their survival in the short term. This step may seem intuitive and self-explanatory. Carnivores would be offered meat. Herbivores will most likely not survive on meat diets, even if they may voluntarily ingest more animal matter than would be expected (Clauss et al. 2016). Because of the flexible nature of most animals, a complete rejection of what is chosen by keepers might be rare. An intriguing example is an experiment with nutria *Myocastor coypus*, a herbivorous rodent, that was described as having a "herbivore creed" that led to a "martyr death by self-inflicted starvation" when an individual was exposed to a non-herbivorous diet (Bickel and Geréz 1936). An important, questionnable aspect of this approach is that 'nutritional wisdom' is ascribed to animals and hence a food item that is accepted is often considered 'right', even though this concept is usually rejected (Kawata 2008; Ullrey 1989). The evolutionary adaptations of animals will only lead to reasonable choices if their environment is identical to that in which the adaptations evolved—for example, in a world without cultivated fruit, grains or (in the case of humans) sweets. Additionally, in order for 'nutritional wisdom' to develop, consequences of a diet must be immediate so they can be related to the diet. While such a feedback mechanism may cause aversion to something bitter, it will not link the negative long-term consequences of obesity to a sweet or fatty taste.

The choice of food items at step 1 is typically from the range of foods available for consumption by humans and agricultural production animals. In composition and concept, nutritional management at this stage resembles either that for farm animals or a human diet. Because of this, the general intuitive acceptance of such diets by humans—curators, keepers, visitors—is high.

Primate diets in particular have contained typical human food items, such as when a gorilla's *Gorilla gorilla* preferred item was sausages (Bickel and Geréz 1936). Experimental work by Remis (2002) showed that when given a choice, zoo gorillas do not choose diet items that have a nutritional composition similar to the food they ingest in the wild, but will choose items of lower fibre and higher sugar content. The parallel to human behaviour is evident. Human dietary habits persisted in zoo animal feeding for a long time, for example including dairy products in the diet of gorillas (Lukas et al. 1999) and the still widespread use of cultivated fruit for many animals that would not find food of this nutritional composition in the wild (Schmidt et al. 2005; Schwitzer et al. 2009). However, most animals will accept these items, which means animals can be kept alive for certain periods of time and may even reproduce. Rare examples of surprising reluctance include when certain herbivores cannot be sustained on grass hay, like giraffes *Giraffa camelopardalis* ssp. and some other browsing ruminants and tapirs *Tapirus* spp. (Clauss et al. 2003; Foose 1982). But these animals accept a variety of other feeds intended for production animals or humans and can be kept alive on these foods for certain time periods. Cases of extreme specialisation that preclude basically all but a single group of diet items, such as koala *Phascolarctos cinereus* surviving only when provided with eucalyptus leaves (Hume 2005), are very rare.

Using carnivores as an example, feeding chunks of muscle meat would be the equivalent of step 1. The term 'carnivore' translates to 'meat-eater' and muscle meat resembles the meat humans acquire for their own cooking and thus is intuitively considered food. The underlying question of step 1 is: What diet will this animal accept? The welfare aspect of step 1 is immediate survival.

Step 2: Meeting nutritional requirements

When animals are kept on items from human or production animal diets, nutritional deficiencies may arise. A classic example is the metabolic bone disease carnivores develop when fed meat—"the original animal model of rickets" (Chesney and Hedberg 2010). Meat without bone contains too little calcium for growth, reproduction and maintenance requirements (Allen et al. 1996). The same problems occur in animals such as primates when predominantly maintained on cultivated fruit (Fiennes 1974) as fruits also contain too little calcium. Similar to the metabolic functions of calcium, insufficient vitamin D_3 production in primates may result in corresponding clinical signs such as rickets, growth impairment and renal failure (Crissey et al. 1999; Yamaguchi et al. 1986). Limited or non-existent ultraviolet B exposure for vitamin D_3 synthesis can lead to vitamin D deficiencies, in particular reported in primates with dark skin pigmentation (Moittié et al. 2022; Ziegler et al. 2018). In contrast, New World monkeys like marmosets require higher levels of dietary vitamin D (Takahashi et al. 1985). A similar logic may apply to other minerals, vitamins and protein or amino acids depending on species and feeds used. Many of these problems were addressed early on in the history of zoo animal nutrition. Herbert Ratcliffe from Philadelphia Zoo was a pioneer in this respect, introducing diets that contained nutrients in calculated concentrations to meet the requirements of specific animal groups. The effect of this change was drastic—animal survival improved with an approximate reduction in overall annual mortality of mammals and birds from 20% to 10% (Ratcliffe 1966). For example, an analysis of museum skeletons demonstrated a historical decrease in the occurrence of metabolic bone disease in zoo baboons *Papio* spp. over time (Sadhir et al. 2022).

This higher survival is also marked by an increase in the occurrence of a disease typical for old age—cancer (Lombard and Witte 1959). Better diets lead to more cancer and most likely other age-related diseases because they allow animals to reach an age where these diseases can develop (Clauss and Müller 2024). And of course, these changes also increase the likelihood of self-sustaining populations.

Thus Step 2 is characterised by a focus on mineral, vitamin and other nutrient supplementation, either in the form of supplements that are applied to deficient food items, as when meat, insects or fruit are dusted with a calcium-containing powder, or in the form of compound feeds (such as pellets, extrudates, sausages) designed as complete feeds or as part of an animal's ration. As long as this step consists of adding supplements to the diet items chosen in step 1, it is typically well accepted by those involved because it combines the acceptance of human and agriculture-derived feeding concepts with the expertise of adding 'a special powder'. By contrast, if this steps consists of adding completely mineralised and vitaminised compound feeds to a diet, it may meet more emotional resistance because such diet items are unduly perceived as 'artificial' (Hediger 1966).

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It is important that nutrient deficiencies are not forgotten. Classic ration calculation is challenging and best left to specialists. It aims to prevent nutrient deficiencies (or toxicities). In terms of animal biology, this step is related to the biochemistry of feeds and animals—something not intuitive for most people working in zoos.

For carnivores, feeding chunks of muscle meat dusted with a supplemental powder or feeding a mix composed of processed meat enriched with minerals and vitamins would be the equivalent of step 2. The underlying question of step 2 is, given the assumption that avoiding deficiencies will allow both reproduction and the raising of healthy offspring: What diet will allow this animal to reproduce? The welfare aspect of step 2 is freedom from deficiency-triggered disease.

Step 3: Meeting physiological needs

Success in step 2 allows focus on more subtle nutritional issues that go beyond basic survival and the prevention of dramatic deficiencies. These aspects refer to diseases or health problems that are less drastic and potentially develop over longer time periods than deficiencies. These problems are, to the authors' knowledge, classically not defined as deficiencies but often referred to as a 'lack' of a certain factor. There do not seem to be any clear-cut definitions to distinguish these. One typical example is the need for structural fibre to foster peristalsis and proper gut function in herbivores, ranging from the sheer issue of a "lack of bulk" (Meredith and Prebble 2017) to problems in colonic separation in coprophagic herbivores (Guerra Aldrigui et al. 2018) or lack of sufficient long-stemmed material for rumination in ruminants and camelids (Mertens 1997). A lack of structural components in processed meat products may lead to calculus formation on carnivore teeth (Bond and Lindburg 1990), which sometimes is countered by sporadically offering bones in addition to processed meat diets. There are potentially beneficial effects of indigestible components for various species, from the soil inadvertently ingested by insectivores (Gull et al. 2015) to the less digestible components of whole prey (Depauw et al. 2013). Finally, there are a suite of civilisation diseases with obesity at the forefront (Morfeld and Brown 2016; Schwitzer and Kaumanns 2001) and including other consequences of consuming energy-dense and often sugar-rich diets, such as malfermentation, acidosis, diabetes, hypertension and hoof problems (e.g. Kuhar et al. 2013).

Step 3 includes a move away from the diet items accepted in step 1 and towards diets that resemble, in chemical composition as well as physical structure, animals' natural diets. Often, this means a departure from long-standing food purchase traditions, requiring more engagement when the step is initiated until the new channels and procedures are well-established. Also, because diet items used in step 1 are often widely accepted, shifting away from them might be a source of social conflict among the personnel involved. As 'more natural' often means 'less palatable' compared to cultivated diet items, the animals might not react positively either.

Step 3 expands the biochemical view of nutrition towards its interactions with large anatomical structures. It is here that considerations about dentition, gastrointestinal anatomy and physiology come into play—factors that are well-known by biologists and those interested in the respective animals, including curators, keepers and informed visitors. Cultural traditions, so to speak, clash with biological logic.

It is at this step that it is recognised that cultivated fruit do not resemble the fruit that frugivores consume in natural habitats (Schmidt et al. 2005; Schwitzer et al. 2009) and that health issues related to sugar, such as obesity and dental caries, can be avoided by removing cultivated fruit from the diet (Plowman 2013). Therefore, whether a zoo is at step 2 or 3 might be assessed from which animals still receive cultivated fruit in their zoo rations. Mimicking natural diets might seem straightforward in some cases, such as providing browse for browsers and whole prey for carnivores, but is less intuitive when it comes to replacing cultivated fruit with green leafy vegetables in the diet of frugivorous primates.

For carnivores, feeding whole prey would be the equivalent of step 3. The underlying question of step 3 is: What diet will guarantee a disease-free, long life? The welfare aspect of step 3 is freedom from long-term compromised physiological health.

Step 4: Meeting psychological needs

In natural habitats, animals perform species-specific behaviours to acquire and process food which have become part of their evolutionary psychological and physiological repertoire. If food is presented in human care in ways that do not foster these behaviours to the same degree—both quantitatively (in terms of the time spent foraging and feeding) and qualitatively (in terms of the specific behaviours performed)—then behaviour at the zoo will deviate distinctively from that in the natural habitat. While time 'freed' in this way may in certain cases allow the animal to express potentially positive behaviours it cannot display in the wild, such as the novelty-seeking and innovative behaviour of orang-utans in human care (van Schaik et al. 2016), the lack of opportunity to perform a behaviour the animal has evolved for mostly leads to either excessive passivity or undesired behaviours such as stereotypies and hence compromised welfare (Bashaw et al. 2007; Britt 1998; Rees 2009). A reduction in, or absence of, undesired behaviours is an intuitive aim, the performance of species-appropriate behaviour can be interpreted as a positive affective state (Gray 2017; Mellor 2016) that is even linked to neurohormonal feedback circuits (Mellor 2015a, b) or as a means of facilitating a meaningful life for the animal, based on the fact that it is provided with opportunities to perform its natural behaviour in ways that have relevance for its life (Clauss and Schiffmann 2022). In terms of feeding, this relevance translates into a system where the animal acquires food dependent on whether it pays attention, focuses or performs work. This means that a decision by the animal to exhibit a certain behaviour has relevance and provides 'meaning', as opposed to a situation where no matter what the animal does, it will always get the food (and hence its behaviour has no meaningful effect on the outcome).

Thus, step 4 puts the focus on a holistic view of both physiological and psychological health in terms of the activity induced by the feeding regime. In other words, modern zoo feeding management addresses typical issues of energy and nutrient requirements, not only structural needs covered by diets, but also behavioural aspects. Ways of addressing this latter aspect are traditionally called 'enrichment'. Although this term is useful, it betrays a past of a less-than-optimal focus on animal welfare—because many things that make life in zoos closer to nature were called 'enrichment', as if one was doing something extra. In reality, not providing most sources of enrichment equals pauperisation, with corresponding negative impact on animal behaviour.

Many examples of discrepancies between natural habitats and zoos are easily understood. At the zoo, a predator is generally not cognitively challenged in terms of securing prey—no matter how it behaves, it will ultimately be presented with food. An elephant that receives its daily ration as a pile of hay (and pellets and vegetables) does not have to move at all once it has reached that pile, in contrast to free-ranging animals that need to move constantly while foraging. A giraffe that can dip its snout into a trough full of pellets and thus grab as large a mouthful as its lips allow will need fewer individual feeding movements than a free-ranging giraffe that must pluck individual leaves from between the acacia's thorns.

In the authors' view, step 4 represents the most recent development in zoo animal nutrition. Whereas the problems encountered during step 3 might often be emotional, those encountered during step 4 are often logistical (in terms of the additional resources required to move from an unengaged to an engaged feeding method). Progress may also be hampered by a lack of behavioural knowledge and a lack of available solutions for practical implementation of potential methods. However, in terms of compliance, the changes necessary for step 4 are expected to meet less emotional resistance than step 3 (unless traditional husbandry methods have become ingrained) because displaying appropriate behaviours should make animals more fascinating to observe and possibly more content.

For carnivores, feeding whole prey in a way that requires cognitive as well as physical activity by the predator would be the equivalent of step 4. The underlying question of step 4 is, adopting the concept of a meaningful life from Clauss and Schiffmann (2022) outlined above: What diet and feeding method will guarantee a disease-free, long and meaningful life? The welfare aspect of step 4 is long-term physiological health with the positive or neutral affective state that comes from needing to perform adequate behaviours to have a meaningful life.

Overview of mammalian feeding behaviour

To have aims for behavioural management, knowledge about the feeding behaviour and activity budget of the animal in question is required. This should be acquired on a species-by-species basis whenever possible. However, some rough guidelines can be outlined using a graph from Hiiemae (2000) (Figure 1).

Small animals can live on comparatively small and spatially distributed items like invertebrates or nectar and find sufficient amounts of these to fulfil their daily energy requirements. Such animals typically search for their food for a large part of the day, which cannot be replicated by offering food once or twice in a bowl. As herbivores (right side of Figure 1) become larger, they have to shift their focus from items that are comparatively rare in the environment (such as seeds) to items that can be encountered everywhere (like grass or tree leaves) so that they can ingest sufficient amounts to meet their daily energy requirements. Along this axis, animals spend a large amount of their active time feeding, which can be mimicked by either feeding them repeatedly during the day—as is common practice in great apes (e.g. Bloomsmith and Lambeth 1995)—or by ensuring forage is available at all times—as is common practice in large hoofstock. As faunivores (left side of Figure 1) become larger, they may still go for comparatively small prey, such as felids hunting rodents or pinnipeds hunting fish. To meet daily energy requirements, a large number of successful individual hunts are necessary, which may be facilitated in pinnipeds by hunting prey that occurs in schools. For terrestrial predators such as a small felid living on rodents, this implies a comparatively large number of successful, individual hunts per day (De Cuyper et al. 2019), which will not be mimicked by one or two daily deliveries of food. For large terrestrial predators such as the tiger, small prey items like rodents are not accessible in sufficient numbers per day; therefore,these animals have to hunt larger prey (Carbone et al. 1999). This can often lead to a situation where these animals do not need to have a successful hunt every day but can gorge themselves to be "full and lazy" (De Cuyper et al. 2019; Jeschke 2007), a situation that is not mimicked by allotting small daily rations or by interspersing fast days in a series of days with small rations (Kleinlugtenbelt et al. 2023). Finally, large omnivores such as bears may use the opportunity offered by special ecological circumstances where they can harvest surprisingly small food items (compared to their own body size) due to the extremely high, lumped seasonal availability of these items such as berries or salmon. Mimicking such feeding is also not feasible with one or two lumped feedings per day.

In conclusion, the feeding patterns of most mammals do not correspond to a one- or two-meal pattern that would best suit daily feeding schedules by zoo personnel. Therefore, methods to dispense food at naturalistic frequencies, ideally without increasing the workload, are required. To the authors' knowledge, corresponding feeding methods are in use for certain species in many zoos.

Case study examples

A detailed catalogue of activity budgets and foraging patterns would be welcome for the development of guidelines for zoo animal feeding, but does not yet exist. Therefore, decisions must typically be made on a species-by-species basis or possibly on the basis of larger animal groups with similar behavioural adaptations. Several measures to achieve more naturalistic feeding behaviour are self-evident, such as distributing food across many different locations, providing food at a higher frequency than once or twice a day, making access to food more challenging both in terms of physical and cognitive effort required to attain it and choosing—from among a variety appropriate for a species—feeds with a lower energy density so that more has to be ingested for the same energy gain. Nevertheless, a variety of examples are briefly mentioned below to inspire curators and keepers to further explore the biology and solutions for mimicking natural conditions to facilitate naturalistic feeding behaviour.

Rabbits Oryctolagus cuniculus

Under natural conditions, rabbits feed for approximately 4–7 hours per day (Mykytowycz and Rowley 1958). By contrast, rabbits fed a complete laboratory rabbit diet spend approximately two hours per day feeding (Olivas et al. 2013). A study with pet rabbits showed that on a hay-only diet, rabbits fed for approximately 10 hours per day, whereas on a muesli mix diet with a higher energy density and without access to hay, the animals fed for only 2.5 hours per day (Prebble et al. 2015a). The rabbits on the muesli mix diet gained more weight and had a more obese body condition whereas all animals grew adequately, irrespective of diet (Prebble et al. 2015b). This example underlines the relevance of diet for the daily activity budget of animals. In the case of rabbits, feeding a roughage-only diet as opposed to a muesli mix or a complete laboratory diet represents a daily difference of up to 7.5 hours during which the animals are either occupied eating or have 'free time'. Over the course of a year, this corresponds to more than 100 days of 'nothing to do'—highlighting the relevance of nutrition for behavioural management of animals. In a professional husbandry system, there would have to be a concept of how the animals are supposed to spend their time if fed on the high-energy diet. These implications reported in rabbits can likely also contribute to appropriate dietary management in herbivorous zoo rodents such as prairie dogs *Cynomys* spp. or hyraxes *Procavia, Heterohyrax* and *Dendrohyrax* spp.

Giraffe Giraffa camelopardalis

Veasey et al. (1996) compared the activity budget of zoo giraffes with that of free-ranging animals. Their data are presented in Figure 2, with additional behavioural data results from other studies. It is evident that during the day (Figure 2A) zoo giraffes spend less time feeding than free-ranging giraffes and show different degrees of stereotyping. Only in a single zoo report on a feeding regime with a very high proportion of browse (Schüßler et al. 2015) were feeding times approximated that were similar to the wild and stereotypies minimised. During the night, zoo giraffe typically ruminate less than their free-ranging counterparts (Figure

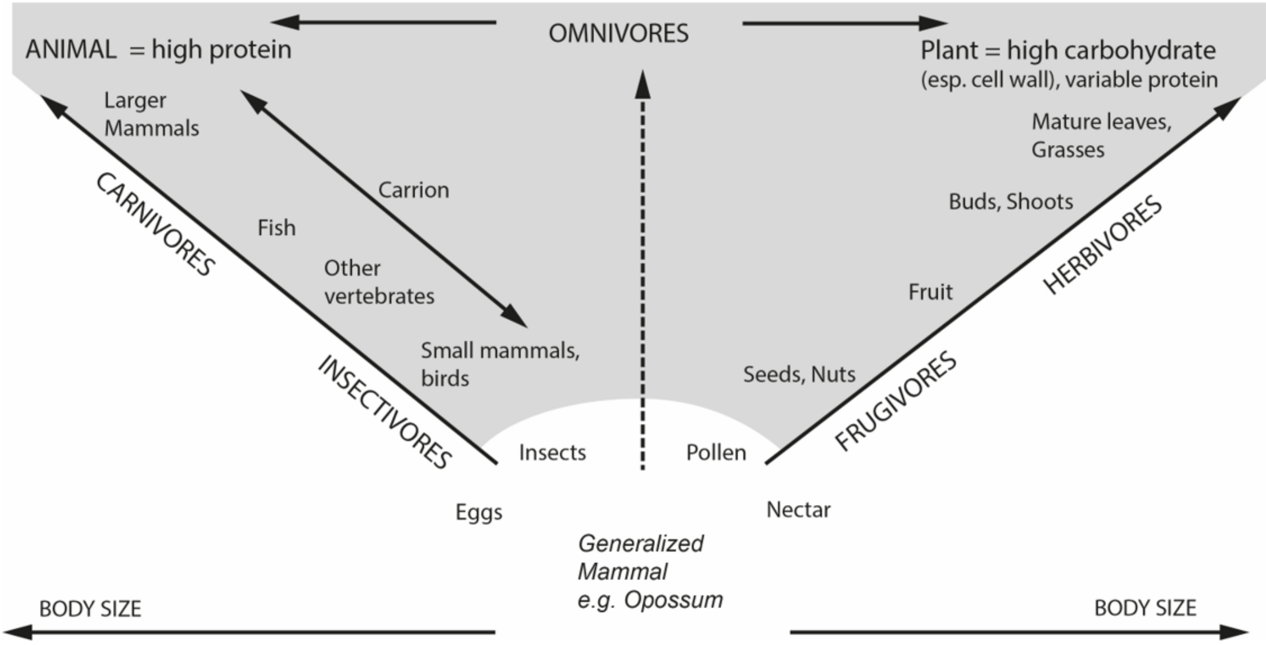

Figure 1. Schematic representation of mammalian body size and trophic group (omnivores in the middle, faunivores on the left and herbivores on the right). The graph indicates changes of diet items with changes in body size across species, from small at the bottom centre to large towards the upper part of the graph. Modified from Hiiemae (2000).

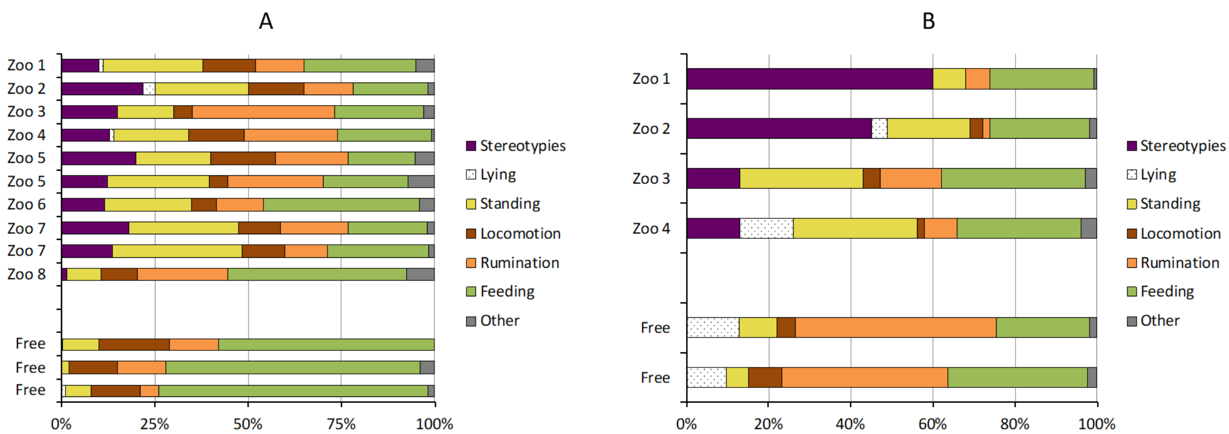

Figure 2. Activity budgets for giraffe *Giraffa camelopardalis* kept in zoos and in a natural habitat for (A) the daytime and (B) the nighttime (Bashaw 2011; del Castillo et al. 2005; du Toit and Yetman 2005; Orban et al. 2016; Pellew 1984; Schüßler et al. 2015; Veasey et al. 1996)

2B). These data give evidence for the difference in activity budgets of free-ranging and captive individuals and provide benchmarks for assessing interventions. As a word of caution, rather than understanding data from the natural habitat as a fixed biological characteristic, it is rather its magnitude that should serve as a guideline.

Equids
Free-ranging plains zebras *Equus burchelli* spend 11–15 hours grazing and 4.5–7.5 hours standing (Neuhaus and Ruckstuhl 2002). In domestic horses kept exclusively indoors, standing time (without anything to do) increased from about 8 hours when animals were fed only hay to about 13 hours when fed only pellets, with an additional increase in searching behaviour to more than 2 hours on the all-pellet diet (Elia et al. 2010). Again, this emphasises the relevance of the dietary regime on behavioural management. In a simple experiment with domestic horses, Ellis et al. (2015) increased the feeding time and reduced the standing time significantly when offering hay in a triple layer of hay nets as compared to using a single hay net. Evidently, reducing the mesh or opening size in nets, racks or similar structures will require more time of the animal to harvest a similar amount of food. Such methods should be applicable to basically all herbivores. In zoo giraffe, this principle has recently been shown to increase feeding times and concomitantly reduce stereotypies (Depauw et al. 2023; Walldén 2023).

Sloth Choloepus hoffmanni
The diet fed to two-toed sloths in zoos differs distinctively from that in the wild; in particular, many items fed in zoos are higher in energy density (Hayssen 2011). At the same time, the reported daily time spent sleeping is 20 hours at zoos versus only 11 hours in the natural habitat (Hayssen 2011). It is tempting to suggest that the reduced requirement to search for food in zoos coupled with the energy-dense diet is responsible for this inactivity. It would be interesting to test whether changing zoo sloth diets towards rations higher in fibre and lower in energy density, as propagated by Bissell (2021), leads to increased activity and hence also to a greater display effect and educative value of sloths.

Hedgehog Erinaceus europaeus
During a single night, hedgehogs must fill their stomach about twice to meet their energy requirements (Yalden 1976). To do so, they move between one and two kilometres per night and spend approximately four hours foraging (Riber 2006). By contrast, a total feeding duration of 22–27 minutes per night was reported for captive individuals (Campbell 1975) and for some captive individuals locomotion stereotypies have been described (Dimelow 1963). Given the large number of hedgehog care centres across Europe, the paucity of newer information on these aspects is surprising. These differences may be representative of other small insectivorous or omnivorous species in captivity, for example armadillos. Comparing reports on nighttime activity in free-ranging (Ancona and Loughry 2009) and zoo armadillos housed in a nighttime enclosure (Kelly and Rose 2024) suggests significantly more foraging and feeding activity in free-ranging specimens.

Giant anteater Myrmecophaga tridactyla
Similarly to many other animals, giant anteaters spend less time foraging/feeding in zoos than their natural habitat (Bertassoni and Milléo Costa 2010). When the time to complete a meal consisting of typical 'zoo gruel' was recorded, zoo anteaters had 15-minute feeding bouts. This can be compared to data on the feeding bout length for captive animals offered different species of actual termites in the form of broken-up material from termite mounds harvested the previous day, which was between 1 and 7 minutes, and to free-ranging animals that break up a termite mound to feed themselves, which averages 21 seconds (Redford 1985). This short duration is explained by the fact that in intact termite mounds, 'soldiers' assemble quickly at the site of breakup, outnumbering the 'workers' and defending the mound with their massive jaws causing the anteater to move towards another mound. Mimicking this aspect of natural feeding behaviour would require many small-portion feedings in zoos. This case is an example that important, interesting and plausible biological facts might shape the behaviour and activity budget of free-ranging animals that one would not intuitively think of; reading the biological literature about the animals kept at a zoo hence is important for developing appropriate ideas.

Primates
Also in primates, comparisons between free-ranging and zoo animals indicate longer feeding and foraging times in natural habitats (Kamaluddin et al. 2022; Melfi and Feistner 2002). Apart from notes on tigers (De Rouck et al. 2005) and giant otters *Pteronura brasiliensis* (Friedmann et al. 2023), to the authors' knowledge it is especially in primates that a positive effect of captivity on behavioural repertoire has been noted, insofar as the safety and 'spare time' in captivity might facilitate novel positive behaviours not displayed in the wild (van Schaik et al. 2016). Nevertheless, increasing the time spent feeding/foraging is still an important aim in primate husbandry. Yamanashi and Hayashi (2011) showed that when captive chimpanzees *Pan troglodytes* had to work for their food through cognitive tests, they spent about as much daily time acquiring their food this way as the foraging time of free-ranging chimpanzees. By contrast, if they were provided the same amount of food during weekends (when the cognitive test devices were not operating), their feeding time was significantly lower.

Diet choice can have an effect on interactions within a primate group. Feeding a fruit-free diet, i.e. a diet with fewer items that might be perceived as 'worth fighting for' due to their sugar content, has been associated with reduced intragroup aggression or vocalisation (Britt et al. 2015; Viallard et al. 2023).

Large carnivores
The last example case touches on a well-known fact: large carnivores do not have 100% hunting success; in other words, when they are motivated to feed they cannot fulfil that motivation instantly but have to try repeatedly. Examples are 20% hunting success in leopards *Panthera pardus* (Balme et al. 2007) and 29% hunting success in lions *Panthera leo* (Balme et al. 2013). These numbers are specific to the respective ecological context of the observed populations and will vary by season, prey and most likely individual predator experience. Hence, they should not be considered 'natural laws' but mainly an indication that a herbivore starting to graze or browse will in most cases be somewhat successful immediately, but a predator may require several attempts to acquire its prey. To the authors' knowledge this has not been replicated in zoos so far—animals are typically 100% sure that they will get the food with which they are presented—regardless of whether access is more or less difficult. To what extent the option to fail and hence the cognitive incentive to focus and the potential of actually 'feeling successful' affects predator behaviour and welfare has to the authors' knowledge not been investigated. Clauss and Schiffmann (2022) propose that the opportunity of failure represents an important aspect of a 'meaningful' life for animals, as an intuitive concept without proof. The only description of a feeding device for zoo carnivores (for cheetah *Acinonyx jubatus*) that withdraws the food if the animals do not pay sufficient attention or make sufficient effort is that of a moving bait zip-line that pulls up the prey after a short period during which it is within reach of the animals (Williams

et al. 1996). However, this study does not explain the overall feeding management, i.e. whether the consequence of a 'failed attempt' is a fasting day or whether the animals will receive the food a bit later anyhow. Designing hygienically sound, escape-safe, technically feasible methods of presenting carnivores with their food (e.g. humanely killed whole prey) in a way that they can periodically fail to obtain the food might represent an attractive next step in carnivore husbandry. Most likely, the experience of failure need not be as frequent as unsuccessful hunting events in the wild to achieve the effect of ensuring full cognitive focus. One possible effect of a task that requires concentrated focus and is experienced as important by the animals might be relaxation afterwards (Krawczel et al. 2005).

Conclusion

Dietary management in a modern zoo requires more than formulation of an optimal diet in terms of ingredients, brands and supplements. As wild animals in captivity have been removed from their ecological context and the necessity to acquire food on their own, it is important to imitate natural conditions to facilitate feeding and foraging behaviour that is appropriate for the species and hence as naturalistic as feasible under zoo conditions. Not everything can be mimicked: for ethical reasons, it is not acceptable to feed live prey and hence other ways of simulating searching, hunting and prey processing are needed. For logistical reasons, it is difficult to provide plant material such as hay in a way that resembles the natural growth form with the resistance of the roots (and hence 'plucking' or 'pulling off' cannot be simulated). It is the task of managers of zoo animals to find creative alternative solutions.

Active application of knowledge on natural conditions and behaviours is essential for improving animal welfare by dietary and feeding management. Following the four-step model described, one could argue that steps 1–3 should be relatively straightforward and therefore fundamental to guarantee high standards of animal health and welfare in zoological institutions. However, the harsh reality is often more complicated; employment of qualified nutritionists is rare and dietary management is challenging because of zoo management restrictions.

Steps in the development of zoo animal nutrition are not made in synchrony across species or zoos. Captive herbivorous ungulates, for instance, will be provided with a herbivorous diet in most zoological institutions (step 1). Moving forward to steps 2 and 3, zoos tend to find formulation of an appropriate nutrient profile for ungulates more challenging. First, the different grazer-browser foraging strategies (Clauss and Dierenfeld 2008; Clauss et al. 2008; Hofmann 1989) are often not implemented due to real or perceived difficulty in obtaining browse, resulting in zoo diets containing inappropriate types of forage or inappropriate cultivated or commercially available feeds. Second, captive herbivores are almost never exclusively provided with food covering their basic requirements, i.e. roughage supplemented with an appropriate pellet, but are offered produce or even biscuits for training. Many zoos prefer adding particularly well-liked (and hence most likely 'unnatural') items for enrichment rather than following a strategy of providing the normal diet in an 'enriched' way. Constraints in terms of obtaining adequate food resources—either due to a lack of finances for the required staff time or a lack of dedication of such staff—will result in a relapse back to steps 1–2, for example evident in limited availability of browse during winter in temperate zone zoos or inadequate roughage quality.

Whenever a zoo does succeed in the formulation of an optimal zoo diet on which the animal will survive and nutritional and physiological requirements are covered, the step 4 challenge of facilitating natural feeding and foraging behaviour arises. Food provision is often restricted to the operational hours of the zoo and feeding management of the animals thus may not account for the majority of their day.

To date, as few as 11 EAZA accredited zoos in Europe employ a qualified nutritionist as a staff member to focus on the nutritional needs of the animals in those collections (Samet and Clauss 2023); based on discussions with these specialists, it is evident that they are often still confronted with issues representative of steps 2 and 3 rather than making progress in step 4. By providing the historical outline of steps in the development of zoo animal nutritional management, the authors hope to inspire zoos to assess where they are with respect to the different animal groups in their care. The case study examples are provided to inspire zoos to venture into timely, plausible solutions for step 4—towards making a major contribution to the welfare of animals in their care, not by adding something to an appropriate diet but by presenting the appropriate diet in a way that makes the life of their animals more meaningful.

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