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Adjusting Our Thinking About Feeding Animals: Fiber as the Metric for Mimicking Natural Diets

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ABSTRACT

Free-ranging animals often ingest markedly different diets than their counterparts under human care, whether companion animals, production animals, or zoo animals. A nutrient with a prominent lack in the diet under human care across species is fiber. Dietary fibers are more difficult to digest than other nutrients and require microbial fermentation, typically resulting in an overall reduction of digestibility and metabolic efficiency. Nevertheless, or therefore, dietary fiber supports health, as it fosters a healthy gut microbiome and limits the risk of obesity and its comorbidities. And due to their lower energy density, high-fiber diets typically increase feeding time, and therefore reduce time available for undesired behaviors. As an adaptation to natural environments replete with high-fiber feeds, humans and animals alike have evolved gustatory preferences for low-fiber, energy-dense feeds. In zoo animal nutrition, the occurrence of both, potentially involuntary feeding of low-fiber diets due to uncritically following feeding traditions, and the deliberate deviation in fiber levels from natural diets, can be documented. Zoo staff appear to transfer their own evolved preference for high-energy feeds to the animals in their care, making zoo animal nutrition a showcase of cultural traditions clashing with biological knowledge. The fiber levels of zoo animal diets can therefore serve as a scale bar for how much zoo management is guided by biological knowledge as opposed to other factors (e.g., anthropomorphism). Increasing fiber levels, possibly to levels observed in the wild, holds great potential for further improvements in the health and behavioral management of zoo animals.

1 | Setting the Scene

Nature is a fibrous place: Martínez-Vilalta et al. (2016) estimated the amount of non-structural carbohydrates—the non-fiber carbohydrates—in terrestrial plants at only about 10% of the total biomass. In other words, about 90% of terrestrial plant material represents fiber—a ubiquitous food source. When expanding the definition of fiber to a functional level, as done below, then also animal-derived food can contain significant proportions of it. The natural diets of many wildlife species are high in fiber—but our human approach to their nutrition often blocks this out, silently accepting, or proactively promoting, diets of lower fiber content. In this contribution, we argue that using fiber levels of natural diets as a guideline or metric for zoo diet design still represents an important progressive step in zoo animal husbandry.

1.1 | A Functional Definition of Fiber

In vertebrate nutrition, fiber is synonymous with dietary components that are difficult to digest. Vertebrates typically do not produce enzymes that digest the cell walls of plants—'fiber'—but rely on a microbiome in their digestive tract to do so; this has led to a fascinating variety of anatomical and physiological adaptations in herbivores (Stevens and Hume 1998; Clauss

Highlights

- Zoo diets are often lower in fiber than those in the wild.
- Mimicking natural fiber levels is a plausible approach with proven health benefits.
- Fiber levels can serve as a metric to gauge how zoos put biological knowledge into practice

et al. 2023). Plant fiber is measured by a variety of analytical approaches, which typically differ between human nutrition with various ways of determining "total dietary fiber (TDF)" (McCleary 2023) and animal nutrition (Van Soest et al. 1991; de-Oliveira et al. 2012). The methods most relevant for zoo animal nutrition are, in our experience, "crude fiber" and the detergent fiber complex with "neutral detergent fiber (NDF)," "acid detergent fiber (ADF)," and "acid detergent lignin (ADL)," even though other analytes can also be of interest (e.g., pectins and fructans; Schmidt et al. 2005). These different fiber fractions differ in terms of fermentability and roles in the digestive process. Additionally, there are physical aspects related to the structure of high-fiber food, such as whole forages, for example, the distinctively longer time animals take to ingest them compared to compound feeds, even if the latter are of the same fiber level (e.g., Müller et al. 2014), which in ruminant science has led to the measure of "physically effective fiber (peNDF)" (Grant 2023).

Here, we do not discuss the merits of different analytical techniques and fiber types, but emphasize that it is important to know the unit one is actually comparing diets with. It is important to realize that many fiber types are "carbohydrates," even though common language use often equates "carbohydrates" with sugars or starches that can also be digested by the enzymes produced by many vertebrates themselves. Therefore, the latter substances are sometimes called the "easily digestible carbohydrates." The functional concept of fiber has also been translated to feed for faunivorous animals—meat products as well as whole prey—where aspects of bone, cartilage, skin, fur, and other components represent material indigestible to the vertebrate faunivore (Depauw et al. 2013; D'hooghe et al. 2025). Further, chitin—as a long-chain polymer—may represent indigestible bulk to some animals, even though chitinases occur in the digestive tracts of several mammals and birds (Jeuniaux and Cornelius 1978). Finally, larger proportions of soil ingested naturally represent indigestible bulk that will have some but not all functional effects of "fiber" (Gull et al. 2015; Bissell et al. 2023).

Across animal species, fiber concentrations in feed typically reduce digestibility (e.g., Edwards and Ullrey 1999; Clauss et al. 2010; Depauw et al. 2013; Hagen et al. 2015), making the feed "less energy-dense." This means that animals have to ingest more of a higher-fiber food to obtain the same amount of digestible energy compared to a lower-fiber food. At the same time, this means that the digestive tracts of animals consuming higher-fiber food will be filled to a higher extent. Both factors make an overconsumption of higher-fiber food with consecutive obesity less likely compared to a lower-fiber food.

1.2 | A Universal Non-Preference for Fiber

The digestibility-reducing effect of fiber makes natural food items of low fiber concentration valuable to basically all animals. Therefore, animals including humans have evolved tastes and preferences for—amongst other nutrients—easily digestible carbohydrates found in low-fiber food (Demi et al. 2021; Yin et al. 2025). Thus, even though the natural diets of most animals and the dietary habits of humans in modern societies differ distinctively, both generally share a preference for low-fiber food. "Palatable," in general, becomes a synonym for low fiber. Great apes, for example, prefer cultivated fruit over vegetables when given a choice (Remis 2002; Verspeek and Stevens 2020), just as humans do (Offringa et al. 2019). This preference is adaptive in environments in which low-fiber food is scarce and therefore a precious resource, unlikely to lead to negative health consequences; by contrast, it becomes maladaptive in environments—like those of industrialized societies—where such food is abundant and readily available (Mennella et al. 2016).

1.3 | Diet Items and Fiber Content

In plant materials like forages (Watts and Chatterton 2004), in cultivated fruit and vegetables (Schmidt et al. 2005), as well as in compound (pelleted or extruded) animal feed (Rothacher et al. 2023), fiber concentrations are typically reciprocal to the concentrations of easily digestible carbohydrates. When comparing diet items, vegetables in general—and especially green leafy vegetables—have higher fiber levels than cultivated fruit (Schmidt et al. 2005; Offringa et al. 2019); forages and browse, in turn, are usually higher in fiber than vegetables (comparing e.g., data from Hummel et al. 2006b with data from Schmidt et al. 2005; Sha et al. 2014). This is generally considered the reason why cultivated fruit are preferred diet items compared to vegetables, and why recommendations to include a certain proportion of fruit in a human daily diet have better compliance than recommendations to include vegetables, even though the nutritive value of vegetables is higher (Offringa et al. 2019).

In animal products or prey, the "animal fiber" level is typically higher in whole prey that contains bones, skin, fur, etc., compared to meat cuts or processed meat (Depauw et al. 2013; D'Hooghe et al. 2025). Although soil ingestion is ubiquitous in wildlife (Beyer et al. 1994), it is particularly relevant in insectivorous animals (McNab 1984; Bissell et al. 2023).

Compound feeds can be designed to contain a large variety of fiber levels; typically, including a higher proportion of forage ingredients or certain byproducts will lead to higher fiber levels than a higher inclusion of grain-based ingredients or fruit (Rothacher et al. 2023).

1.4 | Agricultural Feeding Practices: Feeding for Production

Production animals are typically not kept for optimal health or longevity, but for an optimal compromise between a high

TABLE 1 | (Historical) feeding recommendations for cattle and pigs of different production aims as compared to data for wild cattle or pig.

Species /type	Crude fiber (% dry matter)	Life expectancy (years)
Cattle[a]		
Beef	12	~2
Dairy	18	~4–6
Wild cattle[b]	32	~15–20
	Acid detergent fiber (% dry matter)	
Pigs		
Fattening piglets[c,d]	0.5, 8.5–12.3	~0.5
Breeding[d]	12.3–14.8	~3–6
Feral pigs[c]	20	~4–8

[a](Kamphues et al. 2024).
[b]Banteng *Bos javanicus* (Sastradipradja and Alikodra 1985).
[c](Yao et al. 2025b).
[d](re-calculated from crude fiber recommendations and crude fiber-ADF conversion from Kamphues et al. 2024).

production of meat, milk, or eggs and the longevity required to deliver these products. Because diets of higher energy density typically allow a higher production intensity, such as higher growth rates (e.g., Głogowski et al. 2018), agricultural feeds often include low levels of fiber. For example, fiber is not even mentioned in many traditional feeding guidelines for domestic pigs, with more recent calls to increase fiber levels to improve animal health and welfare (e.g., Grześkowiak et al. 2022). Generally, aspects of animal health are currently linked to fiber provision in production animals (Jha et al. 2019).

Even though our interpretation is speculative, the hypothesis that dietary fiber in agricultural diets is empirically adjusted to the required longevity of the specific animal is exemplified for cattle and pigs in Table 1. We claim that the higher the intended longevity of an individual within a species, the higher the fiber level in its usual diet. This claim matches in effect (though not in causality) the theory of hormesis in relation to caloric restriction, which quite universally increases lifespan across animals (Mitteldorf 2017).

1.5 | Health Problems Associated With Low Dietary Fiber

In the literature on domestic animals, diets lower in fiber are related to a series of diseases or disadvantageous observations. For example, series of experiments with domestic rabbits have shown that low-fiber diets can lead to diarrhea-associated diseases, low feces production including fecal pellets of small size, fast growth, and the use of forage in rabbits increases feeding time and reduces the risk of obesity and several unwanted behaviors (Gidenne 2003; Prebble et al. 2015a; Prebble et al. 2015b; reviewed in Clauss and Hatt 2017; Meredith and Prebble 2017). In domestic horses, dietary fiber and the use of forages can reduce the incidence of gastrointestinal disease (such as gastric ulcers, laminitis, and colic) and unwanted behaviors (Ermers et al. 2023). In pigs, higher dietary fiber levels and forage provision can reduce the incidence of diarrhea as well as of aggressive and unwanted behaviors (Grześkowiak et al. 2022); actually, a recommended treatment for farms affected by piglet diarrhea is to increase dietary fiber levels from a maximum of 5.6% crude fiber in dry matter to up to 6.7% (Kamphues et al. 2024). Providing dietary fiber through grass hay promoted intestinal development in suckling piglets, an important feature to prepare piglets for the challenge of weaning (Yao et al. 2025a). For ruminants, adequate fiber levels are important for the prevention of acidosis (Valente et al. 2017). In domestic dogs and cats, dietary fiber contributes to gut health and obesity prevention (Fahey et al. 2004). A study in domestic cats demonstrated that whole prey, including its animal fiber, leads to a strong reduction in harmful fermentation compounds such as ammonia and biogenic amines, when compared with an extruded diet with less fiber (D'Hooghe et al. 2024).

2 | Past and Present Zoo Animal Nutrition

2.1 | Ingredient Choice

The historical beginnings of zoo nutrition had two bases: human eating habits and agricultural feeding practices (Fens and Clauss 2024). As outlined above, these bases certainly led to diets low in fiber. The first attempts to improve zoo animal nutrition focused on the provision of minerals and protein rather than fiber, and considerations about fiber levels were notably absent in the early design of compound feeds (Ratclffe 1966; Wackernagel 1966). Ever since, calls for higher fiber levels, for a change from cultivated fruit to green leafy vegetables, and a general reduction of easily digestible carbohydrates have been a persisting topic in the zoo animal nutrition literature (Oftedal and Allen 1996; Oftedal et al. 1996; Fens and Clauss 2024).

Apart from nutrient content, diet items for zoo animals are sometimes categorized by their "training value" or "callback value," as a measure how eager the animals are to work for being rewarded with these items (MC, SB, pers. obs.). Because this categorization will mostly follow palatability, a convention is apparent that, irrespective of health concerns and biological appropriateness, the use of low-fiber items is justified by a necessity of having "attractive" training rewards. This even manifests itself by instructions during workshops on zoo animal training to use cultivated fruit or bread as rewards (MP, pers. obs.). If this is done in the context of so-called "medical training" for health checks, the ironical situation ensues that a prophylactic health procedure is based on comparatively unhealthy rewards.

2.2 | Fiber Levels: Conscious Choices

Whereas the low fiber levels in many zoo diets might not have been deliberate but the consequence of intuitive diet ingredient choices made by human caretakers based on their own food preferences, or due to a focus on different nutrient aspects, or simply on palatability, there are surprising examples in the zoo

TABLE 2 | Example for how traditional recommendations can deviate from biological knowledge: Nutrient recommendation for a zoo diet for red panda (*Ailurus fulgens*) as compared in the same source directly against the species' natural diet, bamboo (Nijboer and Dierenfeld 2011).

Nutrient	Target level (zoo diets)	Bamboo (natural diet)
	% dry matter	
Crude protein	18.0	13–27
Acid detergent fiber	10.0	25–64.2

TABLE 3 | Examples of how neutral detergent fiber composition (in % dry matter) of free-ranging primates' diets compare to recommendations for zoo diets for the same taxonomic groups in the same literature source (NRC 2003).

Taxon	Natural diet NDF% NRC (2003) table 3–2 (or table 3–3*)	Recommendation NDF% NRC (2003) table 3–5
Tamarin (*Saguinus*)	18.2	10
Macaques (*Macaca*)	36.8	10
Chimpanzees (*Pan*)	33.6 (35.6–63.7*)	20
Howler monkeys (*Alouatta*)	47.3–54.0	30
Colobine monkeys (different genera)	44.1	30

literature where low fiber levels were deliberately proclaimed as appropriate for a species. This is particularly evident when tabulated values on fiber levels in natural habitats and in recommended zoo diets are given next to each other, and are in conflict.

One such example are the diet recommendations for the red panda (*Ailurus fulgens*) where a discrepancy between zoo and natural diets is evident within the same table (Table 2). Another very prominent example is the chapter on "Carbohydrates and Fiber" in the Nutrient Requirements of Nonhuman Primates (NRC 2003), where such discrepancies are distributed across several tables in close succession in the chapter (Table 3).

In the case of the red panda, no justification is given for the evident discrepancy, but personal information obtained from the authors suggest that the fiber level recommended for zoo diets was already considered a distinct increase for the species, which has a history of even more extreme deviations from the natural diet under previous zoo management (reviewed in Samet et al. 2025); we speculate that there had been reservations against higher recommendations up to the level of the natural diet, possibly due to the fear that these would not meet compliance on the part of zoos. Calls for compound feed for red pandas with a fiber level close to their natural diet had indeed been voiced in the zoo literature as of 1989 (Kock et al. 1989), but the first commercial diet to meet that specification became available only in 2023 (Samet et al. 2025). There is no biological reason to focus on the red panda; it can just serve as an example how slow the process of aligning of zoo diets to natural diets might be. Other such examples can likely be found across many different taxa.

In the case of the primates, the deviation of recommendations from natural diets appears systematic. A series of justifications were explicitly stated to explain why these lower recommendations were made (NRC 2003). We invite readers to inspect these arguments (Table 4); to us, they are not convincing. One consequence of having tabulated values is that nutritionists (like some of us) are very fond of them—such numbers are needed to perform evaluations of designed diets. Zoo nutritionists cherish the NRC nonhuman primate nutrition guidelines specifically for the fact that they provide actual data that can be used to guide diet formulation in a field where such numbers are not available for most other species. Thus, the NRC (2003) recommendations have also been transferred to non-primate species (e.g., Bissell 2021). However, before such tabulated data are used, it may be advisable to check their conceptual background.

In the case of the primates, an intuitive interpretation of the documented situation is that on the one hand, the recommended fiber levels probably did represent—as in the case of the red panda—already a distinct increase compared to feeding practices in many institutions at the time. Thus, a similar strategy to not overtax the recipients of the 2003 recommendations might have been followed to ensure compliance, which would possibly have been compromised by too drastic changes. On the other hand, especially in the case of those primates also often used as laboratory research animals—macaques and callitrichids—the low fiber recommendations could also be interpreted as a choice to not compromise operations and business practices of animal food producers at the time. To our knowledge, grain products are easier and cheaper to source, and more easily processed in extrudate compound feeds, than higher-fiber ingredients. Either way, it is questionable whether written recommendations that are—possibly—understood by their authors as "*a step into the right direction but not yet the final goal*" will be understood by readers in the same vein.

2.3 | Commercial Zoo Diets

Traditional zoo compound feed originated from the "zoo cake" recipes of Ellen Dierenfeld (1932; cited in Dierenfeld 1997) and later Ratclffe (1966) and Wackernagel (1966). Wackernagel's "omnivore" cake (that was also designated for gorillas) and "herbivore" pellet had crude fiber contents of 2.8% and 7.8% dry matter, respectively! Since then, a historical increase in fiber levels can possibly be traced. This process was driven by particularly susceptible species—like the ruminant moose (*Alces alces*), for example (Schwartz et al. 1985). Thus, even though high fiber levels would be beneficial for any ruminant, companies produced higher-fiber products particularly for browsers and even more particularly for moose, yet at the same time marketed (cheaper) lower-fiber products for other ruminants (Clauss and Dierenfeld 2008).

TABLE 4 | A series of justifications for the fact that recommended dietary fiber levels for nonhuman primates were consistently distinctively lower than those of diets consumed by free-ranging individuals of the same or similar taxa (NRC 2003; pp 68–70), together with our comments.

Topic	Justification (verbatim)	Our comment
Preference/Palatability	*It might be necessary for primates to consume higher-fiber foods in a degraded habitat, and a number of studies have noted a tendency for primates to select against highly fibrous plant parts when less-fibrous foods are available.*	Evolved preferences should not be used to indicate an appropriate diet, but must be evaluated in their evolutionary context.
Fiber is important	*There is strong evidence of beneficial roles for dietary fiber in the diets of several orders of herbivorous animals (…), including nonhuman primates, particularly those whose gastrointestinal tracts are specialized for foregut or hindgut fermentation by symbiotic microorganisms (…). In fact, the occurrence of morbidity associated with gastrointestinal disease in captive specimens of these specialist primates has been attributed to the low concentrations of fiber in their diets (…). These concentrations are not intended as minimal requirements for fiber, but represent guidelines for diet formulation that are rational and achievable and appear to be consistent with primate health.*	There seems to be a discrepancy in argument: while the effect of too-low-fiber diets are acknowledged, diets distinctively lower in fiber than natural diets are nevertheless stated as 'consistent with primate health'. Given the ubiquity of primate obesity (Pontzer 2023) and a plethora of resulting pathologies like cardiovascular diseases (Van Mulders et al. 2024), this statement may have lost its credibility today.
Fiber is important	*These concentrations were reported to have desirable effects on gut health and fecal consistency.*	It is unclear whether this is in comparison to even lower-fiber diets in the sense of 'sufficient progress', or in comparison to some objective 'gold standard'.
The wild may not be optimal	*Primate populations that appear healthy and that are reproducing at an expected rate are probably not harmed by a seemingly high fiber intake. At some field sites and sampling times, however, certain primates appear to be just maintaining a viable population. Consequently, fiber levels consumed in the wild may represent maximum levels that still allow for growth and reproduction but may not be optimal.*	This argument calls for a careful individual evaluation rather than a general discrepancy between zoo and natural diets. Given that zoos are typically curtailing reproduction in many primate species (Wallace et al. 2016), this argument rather implies (whether correctly or not) that population control in zoos might also benefit from higher-fiber diets.
Technological aspects	*Complete diets with higher fiber concentrations are difficult to extrude with present technology, and waste is unacceptably high.*	This does not seem to apply in 2025, as commercial diets higher in fiber are on the market. But even if this argument was true in 2003, why would it justify recommendations of 10% for species that consume about 30% in the wild when 30% was considered the technologically feasible maximum?
Comparison with dairy cattle and horses	*Minimum recommended NDF concentrations for dairy cattle of various ages and productive states range from 25-33% of dietary DM (…). … recommended proportions of forage in the total dietary dry matter fed to horses range from 30-100%. Corresponding values for dietary NDF … were not provided.*	Comparing nonhuman primates to production animals (dairy cattle) does not appear appropriate (e.g., no surplus milk production in primates, distinctively higher longevity). The recommendation of 100% forage for horses could easily be transferred into NDF ranges (e.g. 40-60%), which would have yielded higher values than the ones recommended for primates.

Without insider testimony from the industry, we can only speculate that these developments reflected a combination of inertia when it comes to change processes of ingredient sourcing, diet composition, and customer information. Most certainly, the lower palatability of novel higher-fiber products for most animals, especially when compared to lower-fiber products in current use, is a strong driver against higher fiber levels in commercial zoo feeds. Quite similar to the human food market, healthier feed may be more difficult to sell. But whereas this may be easier to understand when humans make diet choices for themselves, it is more difficult to communicate why one makes less healthy choices for animals in one's care that cannot choose for themselves.

The perceived need by members of the zoo community for highly palatable reward items for training has led to the production of low-fiber "training pellets." Further, among commercially available products, diets of nearly every absolute fiber level have been marketed under the label of "high fiber" (MC, GPJJ, SB, MP, pers. obs.). We have observed more than one commercial diet for primates with crude fiber levels of about 10% dry matter sold as "high fiber." But at the same time, there never was a period in zoo animal nutrition when there was a larger variety of commercial, truly high-fiber products available than today.

2.4 | Comparison of Natural and Zoo Diets With Respect to Fiber

Diets of free-ranging and zoo animals have not been compared on a systematic level, but quite a number of taxon-specific comparisons exist. Examples include gentle lemurs (*Hapalemur* spp.) (Feistner and Mutschler 1999), Douc langurs (*Pygathrix nemaeus*) (Schwitzer et al. 2006), black lemurs (*Eulemur flavifrons*) (Polowinsky and Schwitzer 2009), slow lorises (*Nycticebus* spp.) (Cabana et al. 2018a), black rhinos (*Diceros bicornis*) (Helary et al. 2009), greater kudus (*Tragelaphus strepsiceros*) (Taylor et al. 2013b), or tapirs (Clauss et al. 2025).

Comparisons of fecal fiber levels between free-ranging and zoo-managed individuals indicated that zoo animals receiving diets with many non-forage ingredients had lower fiber levels than conspecifics in natural habitats, whereas zoo animals receiving forage-based diets had similar fecal fiber levels as those in free-ranging conspecifics (e.g., Matsuda et al. 2018; Clauss et al. 2025; Sauspeter et al. 2026).

The general result of most of these comparisons is that diets in free-ranging animals have higher levels of fiber. The contributions to zoo animal nutrition that have called for higher-fiber diets—in conference proceedings, case studies, or reviews—are far too numerous to be cited here.

2.5 | Problems and Benefits Associated With Low- and High-Fiber Diets in Zoos

There is a long list of positive consequences when zoo animals were changed to higher-fiber diets (Table 5), which indicates that low-fiber diets are generally linked to poor fecal consistency, difficulty to control obesity, behavioral as well as specific health issues. These reports align with the plausible concept that higher-fiber diets provide more indigestible material, improving fecal consistency and facilitating easier weight management.

Dietary changes will inevitably also affect the composition of the gut microbiome. There is a large number of reports on differences in the microbiome between free-ranging and zoo-managed individuals of the same species (Diaz and Reese 2021), which can most likely, at least partly, be attributed to the shift in dietary fiber level and profile; however, as these authors state, the translation of microbiome composition findings to health status is largely unresolved. Therefore, in spite of widespread claims that microbiome characteristics (such as diversity) are indicators of gut health (e.g., Lawless et al. 2025), we do not review this literature and rather focus on directly observable or clinical results.

A plausible but maybe rarely published effect of higher-fiber diets is the obesity management of individuals that are part of larger groups fed together. In such a situation, the use of highly palatable, low-fiber diet items is likely to result in the monopolization of such items by dominant individuals. Yet, there might be reluctance to take away these items due to concerns that by cutting them out completely, the energy provision to sub-dominant animals and juveniles might be in jeopardy. Here, we give examples of body weight development in two different taxa that were, in their respective zoos, managed as a group all the time (Diana monkeys, *Cercopithecus diana*; Plowman 2013) or partially (spectacled bears, *Tremarctor ornatus*; Gerstner et al. 2016) (Figure 1). In both groups, when a higher-fiber diet was introduced, animals of ideal body weight simply kept their weight, juveniles kept growing, yet obese individuals lost weight and approached an ideal one. This effect is most plausible explained by the fact that animals will eat to meet requirements on food of low to medium preference, but are prone to overconsumption on highly palatable, highly preferred food.

3 | The Way Forward

As stated before, the call for higher-fiber diets for most zoo animals is a constant theme at zoo nutrition conferences (all authors, pers. obs.). In practice, this typically means an increased provision of natural forages, including browse. Very often, this call is supplemented with evidence of a discrepancy between natural diets and those fed in zoos. Evidently, the main obstacle in putting these calls into practice is not an absence of literature, scientific or otherwise. While we should not stop instructing zoo staff on the dramatic differences in fiber and sugar concentrations between wild and cultivated fruits and vegetables, we believe that many people in the zoo community have received the message. Therefore, the main reason for the still widespread use of low-fiber items has been suggested to lie in cultural and psychological rejection of higher-fiber food items that clashes with biological knowledge (Fens and Clauss 2024; Pritchard Moore 2025, 2026), and this perception is shared by all authors of the present review. We understand that the repetition of evidence in favor of higher-fiber diets most likely will not suffice to overcome this resistance, but we suggest that the closeness of zoo diets to the natural diets of the animals can be used, internally in within-zoo education and evaluation, as a yardstick or metric for how much animal husbandry is guided by anthropocentric perceptions or biological knowledge and plausibility. In some cases, historic shifts in the diet for a specific taxon can be traced in the zoo literature, as in tortoises (Ritz et al. 2012), giraffes (Gussek et al. 2017; Martin et al. 2025), or the already mentioned red panda (Samet et al. 2025). While such historical descriptions may be

TABLE 5 | Examples of effects of higher-fiber diets in various zoo animal groups (note that this is not an exhaustive list).

Effect	Taxon	Source
Improved fecal consistency	Primates	Hollihn (1971); Kirkwood (1983); Savini et al. (1999); Nijboer et al. (2006a); Nijboer et al. (2006b); Plowman and Cabana (2019); de Andrade Carneiro et al. (2021); Viallard et al. (2023); Beltrán and Melchert (2025); Bikart et al. (2025); Maaskant et al. (2025)
	Ruminants	Taylor et al. (2013b)
	Tapirs	Clauss et al. (2008); Clauss et al. (2009)
	Felids	Depauw et al. (2013); Kerr et al. (2013)
	Giant anteaters	Wyss et al. (2013); Gull et al. (2015)
	Bears	De Cuyper et al. (2021)
	Pangolins	Lin et al. (2015)
	Manatee	Krajda et al. (2023)
	Sloth	Krajda et al. (2025)
Improved gut motility	Brushtail possum	Wellard and Hume (1981)
Improved weight management	Primates	Plowman (2013); Plowman and Cabana (2019); Zijlmans et al. (2021); Beltrán and Melchert (2025); Bikart et al. (2025)
	Bears	Gerstner et al. (2016)
	Tapirs	Clauss et al. (2009)
	Pygmy hippo	Taylor et al. (2013a)
	Parrots	Veloso et al. (2014)
Improved dental health	Primates	Plowman (2013); Cabana and Nekaris (2015)
Reduction of feeding-related undesired behavior (and an increase of feeding time)	Great apes (R/R)	Cabana et al. (2018b); Barrett et al. (2025)
	Slow lori	Cabana and Plowman (2014)
	Giraffids (tongue play)	Baxter and Plowman (2001); Hummel et al. (2006a); Schüßler et al. (2017); Monson et al. (2018)
	Ruminants	Gerstner et al. (2016)
	Sloth	(Krajda et al. (2025)
	Porcupines	(Dunham et al. (2023)
Reduced antagonistic behaviors/ vocalizations during feeding	Primates	(Britt et al. (2015); Viallard et al. (2023); Bikart et al. (2025); Zoelzer et al. (2025)
Reduced gastrointestinal disease and improved overall health	Primates	Cabana et al. (2018b)
	Viscachas	Gull et al. (2009)
	Cheetah	Whitehouse-Tedd et al. (2015)
	Meerkats	Dobbs et al. (2020)
Decreased costs of feeding	Primates	Plowman (2013)
	Manatee	Krajda et al. (2023)
Improved reproduction	Suid	Diamant 1997, cited in Leus and MacDonald (1997)

considered of little innovative or academic value, they are important tools to showcase changes that have been made, and thus can encourage changes to come. In this respect, every single transition from a lower- to a higher-fiber diet is worth documentation and sharing by publication in the zoo community, because it may well be the sheer numbers of positive examples that may overcome cultural reluctance.

Two aspects often mentioned in defense of low-fiber diet items are the need for variety and the need for attractive rewards for training or "calling animals back" into inside enclosures at the end of a keeper's shift from the outside (MC, GPJJ, SB, MP, pers. obs.). Evidently, the variety argument is easily countered, as variety can also be achieved by offering many different high-fiber items. These might just initially be a bit more difficult to source in a situation where procurement of low-fiber items has a local tradition.

Zoos should encourage food producers to keep and expand their portfolio of truly high-fiber products. By contrast, the production and use of low-fiber products that are labeled "high-fiber" or designated as training rewards should be discouraged.

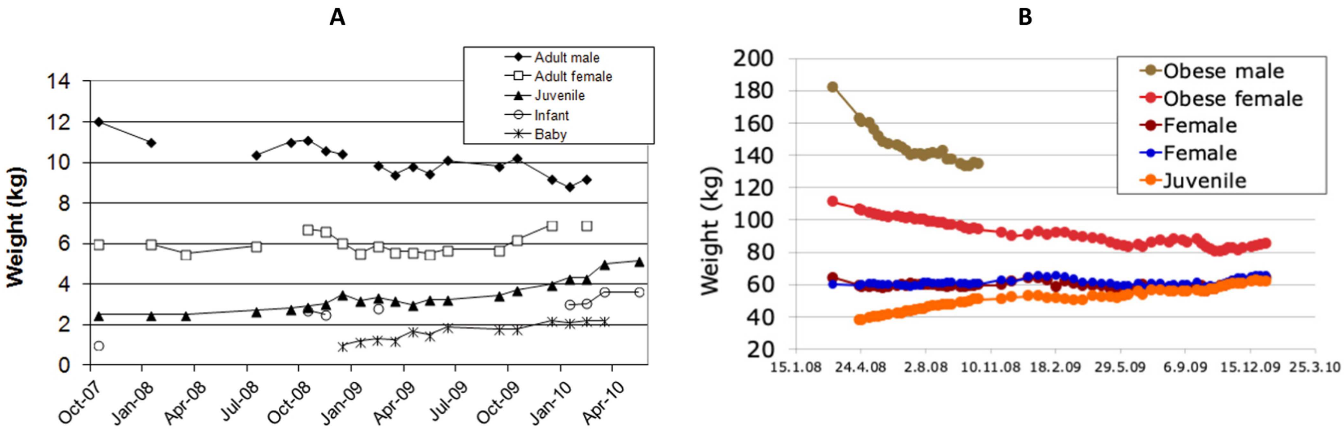

FIGURE 1 | Examples of weight development of animal groups after the introduction of a higher-fiber dietary regime in (A) Diana monkeys (Plowman 2013) and (B) spectacled bears (Gerstner et al. 2016). Note that whereas obese adults lose weight as intended, adults of ideal body weight maintain their weight, and juveniles grow. [Color figure can be viewed at wileyonlinelibrary.com]

With respect to training, our own experiences—though not nil—are more limited. Having spoken to experts in animal training, we suggest that raising children—in which our experience is larger—and training animals share some similarities. It is possible to train children to do their school homework and help in the household by various ways of positive reinforcement. One of these ways is reinforcement by sweets. It works, yet one can argue that it creates the expectation that desired behavior is only performed in exchange for a highly preferred, yet unhealthy treat. Alternatively, reinforcement can be by creating a situation in which healthy treats are effective, or by praise or other positive psychological interaction. Arguably, these latter approaches might also result in individuals more resilient to situations that do not deliver preferred outcomes. In animal management, this translates also into behavioral patterns that other zoos may have to live with after an animal transfer. Choosing highly preferred, unhealthy components as positive reinforcement, such as high-sugar, high-starch, or high-fat items, is an easy but not the only feasible option. The degree of a team's skill in animal husbandry and training may well be judged by how reliably they can call up behaviors in their animals without such high-palatability triggers. For example, unpredictable variability in rewards does not only have academic conceptual support (Watters 2009), but has also in practice been observed to better maintain animal cooperation in training sessions (C. Schiffmann, pers. comm.). An important component for the successful use of lower-palatability rewards is the creation of an environment in which high-palatability items are scarce, that is, not part of the usual diet.

When transferring animals that have lived on lower-fiber items to a higher-fiber diet, coherence of the keeper team and the foresight of animal reluctance to the change are important. As with children, the disappointment of being refused a highly palatable treat should not outweigh the long-term aim of raising healthy and resilient individuals. Keeper teams habituated to obese animals might respond to a drop of body weight to the species 'ideal' range with panic, and advance communication of target weights is essential. Animals not used to high-fiber diets may take several weeks or longer for a transition (Clauss et al. 2025), and teams should be aware that a diet transition is not a project where success or failure is evident after a few days only.

4 | Conclusions

1. Nutritional guidelines for zoo animals should be informed by the fiber levels observed in natural habitats. The similarity of fiber levels between zoo feeding regimes and natural diets is an important metric for the biological adequacy of a zoo's feeding program. Deviations from these levels should only be accepted if carefully justified by plausible biological or medical arguments.
2. Comparative palatability, in the sense of evolved taste preferences, should not be used as a justification for the choice of diet items.
3. Awareness of the demonstrated health threats and behavioral consequences of low-fiber diets must continuously be promoted across the chain of keepers, curators, managers, policy makers, and food producers. This will take efforts to overrule long-lasting zoo feeding traditions and beliefs based on anthropocentrism and livestock approaches.

Author Contributions

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Ethics Statement

This study did not involve the collection of new empirical data from human or animal participants. As it is a review of published studies and ideas, no ethical approval was required.

Conflicts of Interest

The authors declare no conflicts of interest.

Policy on Using ChatGPT and Similar AI Tools

No AI or langauge tools were used in the writing of this article.

Data Availability Statement

Data sharing not applicable to this article as no datasets were generated or analyzed during the current study.

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