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Research article

Fasted and furious? Considerations on the use of fasting days in large carnivore husbandry

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Abstract
Many large mammalian terrestrial carnivores do not hunt every day in their natural habitats, because given the right prey, they can gorge-feed more than their daily energy and nutrient requirements. At the same time, there is a tradition of exposing these species to one or several fasting days per week in zoos. In this study husbandry guidelines for large carnivores were surveyed, and feeding routines recorded in 44 European zoos. Husbandry guidelines did not suggest that fasting days should be preceded by gorge-feeding, and the most common practice observed at the zoos also did not include a gorge-feeding day prior to the fasting day. This raises the question why fasting days are implemented in zoo regimes in the first place. The observed practice of providing special enrichment on fasting days might stem from the impression that animals are not at ease when fasting after receiving a food portion basically corresponding to little more than their daily requirement on the day before, without a feeling of satiety related to gut distension. These current feeding regimes of zoo carnivores should be re-assessed. The combination of fasting days with preceding gorge-feeding, together with strenuous physical activity and cognitive challenges linked to the feeding event, might have the potential to mimic natural behaviours more closely than current practices. This should be investigated in future studies.

Introduction

In zoos, large mammalian terrestrial carnivores are conventionally fed on a daily basis (Meyer-Holzapfel 1968). Large zoo carnivores also often engage in pacing and repetitive stereotyped motor patterns (Carlstead et al. 1991; Clubb and Mason 2003; Meyer-Holzapfel 1968; Shepherdson et al. 1993), which have been linked to discrepancies between the zoo feeding regime and feeding in nature (Veasey 2017), amongst other causes. In contrast, their free-ranging counterparts neither have a fixed feeding schedule nor eat daily (Altman et al. 2005; Bosch et al. 2015). For example, Schaller (1972) reported that lions eat at an average frequency of once every 2.5 days on plains and once every 3–3.5 days in woodlands; however, hunting success rates vary a lot within seasons and habitats. In their review, De Cuyper et al. (2019) showed that kill frequency is not necessarily linked to carnivore body size, i.e. there is no consistent decrease of carnivore feeding frequency with species' body mass.

Rather, feeding frequency depends on predator body mass range and the size of the prey habitually taken as a species, in a specific habitat or at a specific time of year. For example, whereas several large cats and hyenas typically hunt comparatively large prey that will surpass the daily intake capacity of the predator (De Cuyper et al. 2019), similar-sized brown bears *Ursus arctos* can feed on comparatively small prey items of which they ingest a large number during a day, like salmon or berries (Rode et al. 2001; Welch et al. 1997). Whenever large carnivores subdue large prey and conditions are favourable to gorge-feed (i.e. until the limits of their maximum gut capacity are reached), they can ingest energy in excess of their daily requirements within a short period of time

(De Cuyper et al. 2019). Thus, if they are not in a metabolic state of accruing body stores for periods of hibernation, large carnivores in natural habitats do not necessarily have to hunt every day, allowing them to be 'full and lazy' (Jeschke 2007).

To the authors' knowledge, fasting days are part of a regular schedule in large carnivore zoo husbandry for many species. Allen et al. (1996) state that 'many zoos fast their large cats 1 day per week', suspecting that, even in the absence of scientific evidence, 'occasional fasting is probably beneficial for animals that receive little exercise and are prone to obesity'. Data on the frequency of use of fasting days, and on specifics of their implementation, are lacking. During a larger survey on large carnivore husbandry in 44 European zoos, the peculiarities about the use of fasting days outlined in the present study were noted. These peculiarities led the authors to investigate whether husbandry guidelines recommend fasting days and describe how they should be implemented. The use of fasting days reveals how a zoo's husbandry can match or deviate from conditions encountered in natural habitats, questioning the biological background of such husbandry decisions.

Methods

Husbandry guidelines survey

Husbandry guidelines were collected from the internet, using genus and species names together with the words 'guidelines' as search terms. Guidelines that covered large carnivores were scrutinised for recommendations of fasting days and the results were documented in tabulated form.

Zoo survey

This study is part of a bigger study which was conducted with the support of the EAZA Felid TAG and Canid and Hyaenid TAG (Kleinlugtenbelt et al. 2023). Data from 44 zoos in 7 countries were collected and compiled during personal visits by CLMK; one zoo sent their information in since a personal visit was not possible due to COVID-19 restrictions. The following species were observed during feeding: tigers *Panthera tigris* (26 zoos), lions *Panthera leo* (31 zoos), jaguars *Panthera onca* (7 zoos), leopards *Panthera pardus* (15 zoos), snow leopards *Panthera uncia* (13 zoos), cheetahs *Acinonyx jubatus* (15 zoos), lynxes *Lynx lynx* (16 zoos), hyenas *Crocuta crocuta* and *Hyaena hyaena* (11 zoos), wolves *Canis lupus* (16 zoos), brown bears *Ursus arctos*, including one brown bear–polar bear hybrid (15 zoos) and polar bears *Ursus maritimus* (12 zoos). The responsible staff members were followed on their daily routines with the selected species, both from behind the scenes and from the point of view of a visitor. During personal interviews with the responsible staff members, more information about carnivore feeding regimes, schedules and methods was gained. The interview was based on a pre-planned set of questions but was conducted as a free-flowing conversation rather than a structured listing of the individual questions. All interviews were conducted by CLMK and feeding was documented with photos and videos.

Results

Husbandry guidelines

Twenty-four husbandry guidelines were found for 25 large carnivore species, with the majority of guidelines originating from recognised organisations such as the European Association of Zoos and Aquaria (EAZA) and the Association of Zoos and Aquariums and its Species Survival Plans (SSPs) (Table 1). Generally, fasting days are suggested in husbandry guidelines as part of feeding schedules for several large carnivores (all large felids, spotted hyena, grey wolf, red wolf *Canis rufus*, dhole *Cuon alpinus* and polar bear). Typically, one or two fasting days are recommended per week, and two fasting days per week are repeatedly stated as a maximum.

Some guidelines explicitly state that fasting days are not essential (cheetah: Marker and Schumann 1998; lion: Hillermann 2009), do not mention fasting days at all (American black bear *Ursus americanus*: Lubiw-Hazard 2000; maned wolf *Chrysocyon brachyurus*: SSP 2007a; polar bear: AZA Bear TAG 2009) or discourage fasting days (brown bear: Lorenzo 2009; sloth bear *Melursus ursinus* and sun bear *Helarctos malayanus*: AZA Bear TAG 2019).

Whenever suggested, fasting days are reported to be beneficial for obesity management, or as an opportunity to feed bones and/or small whole prey for dental health, enrichment and nutritional purposes. The feeding of bones on fasting days is recommended repeatedly.

Whereas some texts imply that fasting days serve to mimic natural foraging behaviour (feast and famine), others specifically state that they do not fulfil this function. Only one (cheetah, EAZA 2018) out of 24 husbandry guidelines mentioned specific guidelines for the feeding practices preceding the fasting day, i.e. the necessity to gorge-feed before the fasting day in order to obtain positive effects on carnivore behaviour and avoid an increase in abnormal stereotypic behaviour. For dholes, an alternating feeding regime of feeding and fasting days is suggested with a corresponding increase in the amount of food on the feeding days (EAZA 2017). Other guidelines for tigers (Dierenfeld et al. 1994) and cheetahs (Marker and Schumann 1998; SSP 2009) suggest that whenever fasting days are implemented, the daily ration *on all feeding days* should be increased, to compensate for the energy intake that is lost during the fasting days.

Zoo survey

The majority of zoos used fasting days for felids, hyenas and wolves, but not for brown or polar bears (Table 2). Of those that used fasting days, many performed animal training on these days that included a food reward, especially with leopards—in 53% of the zoos keeping them. Gorge feeding prior to the fasting day was used by a minority of zoos—in 13% of those that kept lions, 8% of those that kept snow leopards, 6% of those keeping wolves and 4% keeping tigers. For all the other included species, no gorge-feeding regimes were in place in connection with fasting days. During interviews, it was sporadically mentioned that the training performed during fasting days partially served to compensate for an increased propensity to stereotype on these days.

Discussion

The results are remarkable because they appear to point out a discrepancy between husbandry recommendations and zoo management practice on the one hand, and the respective animals' natural lifestyle on the other hand. This raises the question why fasting days are used in zoo carnivore husbandry in the first place. An important limitation of this study is that the reasons behind the use of fasting days were not specifically requested, and therefore it is only possible to speculate that use of fasting days is due to tradition at the respective facilities.

For the omnivorous or insectivorous members of the Carnivora, like maned wolves, sloth bear, sun bear, black bear and brown bear, fasting days do not seem appropriate and are consequently also not part of the husbandry recommendations (Table 2). Gorging with a subsequent fasting day on fruit or insects has not been reported in the wild, and even though the hibernating bear species are known for high food intakes at the time of fat accretion for hibernation (e.g. Hilderbrand et al. 1999), this does not lead to fasting days spent only digesting. In hibernators such

Table 1. Summary of fasting day recommendations from husbandry guidelines.

Species	Fasting day recommendations	Source
Tiger *Panthera tigris*	One or 2 fasting days/week improve appetite and body condition On fasting days, large bones can be fed for dental health and as enrichment Two fasting days/week during which bones can be fed for dental health/enrichment Fasting days during which large bones and whole prey can be fed to stimulate the gastrointestinal tract and avoid impaction Fasting days do not reflect wild gorge-fasting foraging behaviour	Dierenfeld et al. 1994 Baker 2006 AZA Tiger SSP 2016
Lion *Panthera leo*	Fasting days are not essential Example of two fasting days/week with chicken neck feeding on second fasting day Fasting days of less than 24 hours are common in many zoos Animals should not be fasted more than 2 days/week	Hillermann 2009 AZA Lion SSP 2012
Jaguar *Panthera onca*	Fasting days of less than 24 hours are common in many zoos Fasting days do not reflect wild gorge-fasting foraging behaviour Fasting days are useful for body weight management Bones can be fed during fasting days Fasting days of less than 24 hours are common in many zoos Animals should not be fasted more than 2 days/week	EAZA 2022 SSP 2007b AZA Jaguar SSP 2016
Snow leopard *Panthera uncia*	Recommendation of weekly fasting On fasting days, large bones can be fed for dental health and as enrichment Fasting days are useful for body weight management	Alankar 2014
Clouded leopard *Neofelis nebulosa*	Recommendation of 1 or 2 fasting days/week On fasting days, large bones and small whole prey can be fed	SSP 2000
Cheetah *Acinonyx jubatus*	Previous recommendation of 1 fasting day/week, however, no proof of health effects Fasting days do not reflect wild gorge-fasting foraging behaviour Fasting days without preceding gorge feeding day might be contraindicated	EAZA 2018
	One or 2 fasting days/week improve appetite and body condition Large bones can be fed on fasting days for dental health Recommendation of 1 fasting day/week and an increase of meal size on feeding days Fasting days might be contraindicated and cause stress Recommendation of 1 fasting day/week and an increase of meal size on feeding days Fasting days are not essential One or 2 fasting days/week improve appetite and body condition Large bones can be fed on fasting days	SSP 2009 Marker and Schumann 1998
Eurasian lynx *Lynx lynx*	Recommendation of 1 or 2 fasting days/week	EAZA 2004
Spotted hyena *Crocuta crocuta*	One or 2 fasting days/week are useful for body weight management On fasting days, large bones and small whole prey can be fed	Foote 2014
Large canids (coyote *Canis latrans*, red wolf *Canis rufus*, gray wolf *Canis lupus*, Mexican gray wolf *Canis lupus baileyi*, maned wolf *Chrysocyon brachyurus*, dhole *Cuon alpinus*, African wild dog *Lycaon pictus*)	Recommendation of 1 fasting day/week for red wolves Varying feeding regimes (feast and famine) for enrichment	AZA Canid TAG 2012 Laidlaw 2000
Gray wolf *Canis lupus* Dhole *Cuon alpinus*	One fasting day/week is useful for body weight management The more food dholes get, the more fasting days they should get Feeding every other day and simultaneously increase the daily meal size	EAZA 2017
Maned wolf *C. brachyurus*	No fasting days mentioned	SSP 2007a
Polar bear *Ursus maritimus*	No fasting days mentioned Several zoos implement at least one fasting day/week	AZA Bear TAG 2009 Lintzenich et al. 2006
Sun bear *Helarctos malayanus*	Fasting days are not appropriate	AZA Bear TAG 2019
Sloth bear *Melursus ursinus*	Fasting days are not appropriate	(AZA Bear TAG 2019)
Brown bear *Ursus arctos*	Fasting days are not appropriate	Lorenzo 2009
American black bear *Ursus americanus*	No fasting days mentioned	Lubiw-Hazard 2000

Table 2. Frequency of different kinds of fasting regimes at 44 European zoos.

Species	No fasting		Fasting day with training incl. food reward (no preceding gorge-feeding)		Fasting day without *any* food preceding gorge feeding			
					no		yes	
	n zoos	%	n zoos	%	n zoos	%	n zoos	%
Tiger	3	12	11	42	11	42	1	4
Lion	3	10	12	39	12	39	4	13
Jaguar	1	14	0	0	6	86	0	0
Leopard	1	7	8	53	6	40	0	0
Snow leopard	4	31	2	15	6	46	1	8
Cheetah	5	33	4	27	6	40	0	0
Lynx	5	31	3	19	8	50	0	0
Hyena	4	36	1	9	6	55	0	0
Wolf	2	13	4	25	9	56	1	6
Brown bear	13	87	0	0	2	13	0	0
Polar bear	11	92	0	0	1	8	0	0

as black, brown or polar bears, food reduction and fasting can be used to initiate hibernation, as indicated by various accounts of bear keepers as well as analysis by Krofel et al. (2017) who showed that the denning period of hibernating brown bears is negatively related to their access to food. In these species, fasting should probably not be used during times of maintenance or during pre-hibernation accretion of body stores. The same applies most likely to many small carnivores, including small felids, which are considered to hunt and eat several times per day (Bosch et al. 2015; Bradshaw 2006).

By contrast, many large felids, hyenas and canids are known to often have an alternating pattern of more active hunting, gorge-feeding days and days spent resting and digesting (see Introduction). Therefore, at first glance, the inclusion of fasting days in the husbandry management of many large carnivores might appear as an attempt to simulate conditions the animals experience in their natural habitats. On second thought, however, both the justification of the fasting days in husbandry recommendations and the actual husbandry practice speak against this interpretation.

Several husbandry guidelines state explicitly that fasting days in zoos do not reflect the gorge-fast situation in natural habitats. Rather, the main reason given for the use of fasting days is obesity control. This leads to the evident question why obesity control should be achieved by implementing fasting days rather than by an overall adjustment of the (daily) amount of diet fed. To the authors' knowledge, there is no literature on zoo carnivores supporting either concept. In human medicine, several recent reviews (most likely all covering a similar range of original studies) have concluded that intermittent fasting is no more or less efficient at reducing obesity than an equivalent diet restriction with daily food intake (Rynders et al. 2019; Stockman et al. 2018; Varady et al. 2022; Welton et al. 2020). Thus, the reason why fasting days are mentioned in husbandry guidelines appears somewhat obscure and might simply be reporting the traditional use of this measure.

The feeding practice observed in most zoos indicates that fasting days are not used as part of a concept that tries to mimic the gorge-fast rhythm in natural habitats, because there is neither a widespread emphasis on increasing the amount of food nor the amount of physical exercise and cognitive challenge on the day before fasting days. On the contrary, rather than focussing increased attention on the day before, it appears that with an emphasis of bone feeding (guidelines) and training with food rewards (survey) on the fasting day, both extra food and cognitive challenges are deliberately provided on this day, as if this day required a special programme. Rather than representing a day of rest after a preceding gorging and physical and cognitive exhaustion, the fasting day seems to represent a day of unrest that needs to be buffered.

Few studies have investigated the effects of fasting days; mostly, these included a gorge-feeding event prior to the fasting day, albeit without a particularly physically or cognitively challenging feeding method (Altman et al. 2005; Finch et al. 2020; Höttges et al. 2019; Lyons et al. 1997). These studies found changes in energy intake and body condition due to a change in the total amount fed per week under the new feeding regime—an effect not actually related to the fasting day, but to the weekly amount fed (Altman et al. 2005). The behavioural changes due to the gorge-fast feeding regime differed between studies, most likely due to additional details such as the time of day food was provided or animal group size and composition. In some cases, animals paced more on feeding days (feeding in the afternoon), interpreted as anticipatory pacing with animals perceiving cues that it was a feeding day (Altman et al. 2005). In other cases, animals paced more on fasting days (Höttges et al. 2019; Lyons et al. 1997). Two studies that compared a conventional and a gorge-fast feeding regime in the same animals found no change (Altman et al. 2005) or an overall decrease in pacing with the gorge-fast regime (Finch et al. 2020). In the latter case, the difference was not noticeable immediately after the diet change, but rather when assessed a second time 12 months after the change.

Höttges et al. (2019) illustrate a potential source of confusion when talking about zoo carnivore feeding regimes: in that study, animals were observed to feed during the so-called 'fasting'

days—because of food items left over from previous days in their enclosure. In the case of large carcass feeding in a gorge-fast schedule, the carcass may be too large to be consumed by the animals in a single day. Höttges et al. (2019) refer to Eloff (1984) as a source for the fact that guarding a carcass, and eating repeatedly from it, can be considered a natural behaviour in the species in question, lions. If animals can still remove relevant portions of carcasses beyond only bone on the following day, this day should not be called a 'fasting' day even if no additional food is provided; this term is best reserved for days where the animals do not have the opportunity to consume food. Given that it may be logistically difficult to remove bones or skeletons from enclosures, a fasting day thus may well mean that the animals occupy themselves with those leftovers that would not be considered nutritious prey components. Such a sequence of events might additionally encourage the consumption of less digestible carcass components like skin, cartilage and bone, which may have beneficial physiological effects for carnivores (Depauw et al. 2012, 2013; Lindburg 1988).

Daily feeding of energetically adequate, yet correspondingly small amounts of food to large carnivores might never cause the distension-linked satiety feeling these animals experience in natural habitats after successfully subduing large prey (Veasey 2017). One study claimed that a gorge-fast regime with whole carcasses for gorging attained this kind of satiety (Höttges et al. 2019). They suggested that this was indicated by a clear difference in behaviour between gorging and fasting days, as opposed to no between-day differences in behaviour on a feeding regime that included one fasting day without preceding gorge feeding (Höttges et al. 2019). The relevance of filling the gut up to its limit for alternating fasting and feeding days was theoretically derived from gut capacity and prey energy estimated by De Cuyper et al. (2019); this concept can also be illustrated using the data presented by Elliott et al. (1977) for the relationship between the size of a meal and the initiation of the next search for prey in lions (Figure 1). These data indicate that a small-sized meal, as would be a typical daily large carnivore zoo ration, would not be followed by an absence of hunting activity on the next day. Feeding large carnivores such daily rations and then exposing them to a fasting day might thus even be the opposite of mimicking natural conditions.

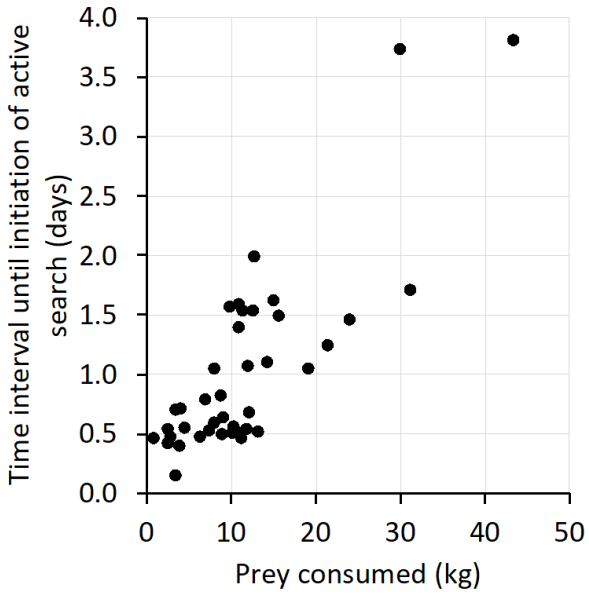

Figure 1. Relationship between the amount of prey consumed for a lion *Panthera leo* and the time until the next search for prey is initiated. Data extracted from Elliott et al. (1977) and converted from hours into days, and from calories into kg, using the given conversion factors. When consuming less than 10 kg of prey, the next search was initiated within a day. Note that due to different energy expenditure between free-ranging and zoo-managed lions, the amount of prey consumed cannot be considered a recommendation for zoo animals; however, the data serve to illustrate the amount of prey considered to cause gut fill-related satiety with a consecutive 'lazy' day.

Another aspect relevant to the effect of feeding on the overall behaviour and activity budget, especially on fasting days, might be the level of physical exercise and cognitive challenge linked to feeding. For example, observations that some (but not all) large felids on a gorge-fast feeding regime paced more on the feeding day after they had been fed (Lyons et al. 1997) could be considered indication that some animals might lack physical activity in relation to feeding. To the authors' knowledge, no studies evaluating the contribution of physical activity (or cognitive challenge) linked to feeding exist for zoo carnivores. The study by Krawczel et al. (2005) on circus tigers, corroborated by personal observations for another set of tigers from another circus by MC, might provide some inspiration for such investigations. These observations were not made in relation to feeding, but in relation to possibly the most exciting moment of the day for the tigers—their performance. Krawczel et al. (2005) describe increasing levels of anticipatory pacing as the moment of performance approached, and basically extreme relaxation or resting afterwards. Transferring these observations to feeding methods in zoos would mean making a gorge-feeding event physically and cognitively challenging, which might increase the difference in behaviour between feeding and fasting days. This would have to be tested in future studies. In this endeavour, it may be particularly challenging to combine gorge-feeding, which is mainly feasible when feeding large carcasses that are conveniently just placed in the enclosure, with physical and cognitive activity. This represents a major challenge and opportunity for innovative feeding methods.

In conclusion, the common practice exposing zoo carnivores to fasting days without a preceding gorge-feeding event should be re-evaluated. Developing and assessing feeding methods that combine gorge-feeding with physical and cognitive challenges may be an important next step in large carnivore husbandry.

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