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Research article

How does feeding regime affect behaviour and activity in captive African lions (*Panthera leo*)?

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Abstract

Lions (*Panthera leo*) are popular zoo animals and obligate carnivores. In the past, zoos focused on the nutritional aspect of feeding, whereas today they also aim to encourage naturalistic feeding opportunities. AZA's Lion Care Manual recommends a frequent feeding schedule, while other sources highlight the benefits of unpredictable, infrequent feeding schedules. Further, the husbandry guidelines for lions by EAZA propose to feed lions separately. To assess how lions are affected by feeding frequency, we collected data on five event behaviour categories (social affiliative, agonistic, exploratory, marking, maintenance) and four state behaviour categories (inactive, active, feed, pace) of four captive lion prides held on either high frequency (HF: feeding pieces of meat on four to five occasions per week) or low frequency feeding (LF: feeding a whole carcass on one occasion per week). We found that some event behaviour categories (agonistic, exploratory and marking) and one state behaviour (feeding) were more frequent for lions on HF feeding. Lions on both feeding regimes engaged more often in agonistic behaviour and were more inactive on feeding days than fasting days. On fasting days, activity and pacing, as well as exploratory, maintenance, marking and social behaviour, were more frequent than on feeding days. During the consecutive fasting days, the lions on LF feeding were increasingly active in terms of walking, trotting and running. The results show that LF feeding with whole carcasses allowed the prides to resolve social discrepancies during feeding, which reduced aggression between feedings. LF feeding resulted in satiety of the lions to the extent of altered behaviour during feeding day and the first fasting day, whereas lions on HF feeding showed unvarying behaviour during feeding and fasting days suggesting a lack of satiety.

Introduction

Lions (*Panthera leo*) are one of the most popular species kept in zoos. In the wild, these social cats live in fission-fusion societies where members of a pride disperse and meet again to feed, mate or hunt communally (Schaller 1972; Bradshaw 2016). In captivity, lions are kept as pairs or small groups in enclosures considerably smaller than their territories in the wild (Shoemaker et al. 1997; Schaller 1972; Haas et al. 2005; Mosser and Packer 2009).

Wild-living lions hunt opportunistically with a success rate of 40% (Eloff 1984). They are known to feed every 1.5 to 2.5 days but have been observed fasting for up to eight consecutive days (Eloff 1984; Altman et al. 2005). In the wild as well as in captivity lions have been reported to spend most of their time inactive (Haas et al. 2005; Young et al. 2013). However, lack of hunting opportunities and onset of boredom in captivity can increase levels of inactivity and may lead to obesity and, consequently, compromised welfare (Altman et al. 2005).

The guidelines of the American Association of Zoos and Aquariums (AZA) recommend feeding large felids with horse meat, beef or processed commercial diets on five days of the week, and to offer bones to gnaw on during the fasting day(s) to ensure dental health, and to vary the diet by occasionally feeding rabbit or chicken carcasses (Shoemaker et al. 1997). The Lion Care Manual of AZA alternatively suggests a daily diet for lions without any fasting days and recommends offering daily feeding enrichment (e.g. bones, horsetails or chunk

Table 1. Overview of pride size, sex composition, average age, exhibit size, feeding schedule (HF = High frequency feeding; LF = Low frequency feeding) and amount of food per week and animal in the four zoos.

Zoo	Borås	Copenhagen	Givskud	Kolmården
Pride size	3	7	12	9
Sex (male: female)	1.2	4.3	1.11	2.7
Mean age (±SD years)	10.3 (±1.2)	2.6 (±1.5)	4.9 (±2.0)	4.2 (±2.5)
Exhibit size (m^2)	2 150	703	50 000	25 000
Feeding	HF	HF	LF	LF
Average amount of meat per week and animal (kg)	> 24	> 24	~ 33.33	~ 33.33

meat) (AZA Lion Species Survival Plan 2012). Although wild-living lions feed together at the same carcass, the European Endangered Species Program (EEP) husbandry guidelines recommend feeding Asiatic lions (*P. leo persica*) separately to "reduce the likelihood of fighting" (Dorman 2010).

These guidelines appear to be contradicting the Standards for the Accommodation and Care of Animals in Zoos and Aquaria formulated by the European Association of Zoos and Aquaria (EAZA 2014), which state that:

1. Animals should be encouraged to engage in as much natural behaviour as possible. Behavioural as well as physiological needs should form the base for a suitable diet.

2. Special circumstances like fasting days/longer periods of fasting need to be considered in the feeding schedule.

3. Natural feeding behaviours should be stimulated and feeding time should preferably last as long as in the wild.

4. Social aspects should be considered when feeding.

In practice these four aspects are often not met (Clubb 2001). The conventional regime of separate and frequent feeding of lions has been found to be sufficient for nutritional purposes, leads to successful breeding and provides a practical maintenance routine for animal keepers (Clubb 2001; Dorman 2010). However, feeding should not be restricted to nutritional considerations but also focus on behavioural and psychological aspects of feeding (as reviewed by Kawata 2008). Whereas several studies have investigated how captive lions behave while feeding, a few studies have assessed how feeding frequency affects behaviour of captive lions both during and between feeding occasions (Roe and Cleave 2005; Altman et al. 2005).

It was therefore the aim of the present study to assess how the behaviour and activity of lions kept on a high frequency (HF) feeding regime differs from the behaviour and activity of lions kept on a low frequency (LF) feeding regime. More specifically, we assessed the frequency of five different event behaviour categories (social, agonistic, marking, exploratory, maintenance) and the frequency of four different state behaviour categories (active, inactive, feed, pacing) and compared them between the two feeding regimes. The study included four zoos, two of which kept their lions on HF feeding while the other two kept their lions on LF feeding.

Table 2. Event behaviour ethogram

Category	Behaviour	Description
Social	Nuzzle	Individual pushes or rubs its head against conspecific.
	Allogroom	Individual licks, bites or chews on another conspecific's fur.
	Social sniff	Individual sniffs anogenital or nose region of another conspecific.
	Mount	A male lion attempts intromission by straddling over the female with front and hind feet.
	Social play	Two or more individuals engage in playful wrestling without visibly hurting each other.
	Stalk	Individual crouches down and stares at conspecific. Might include movement toward target individual.
Marking	Roar	High intensity call that consists of a "main call" and grunting sounds. Usually initiated by male, females might or might not join.
	Claw	Lion drags front claws along an object or surface, likely leaving visual marks behind.
	Urine spray	While standing with tail raised vertically or crouching with tail held parallel to the ground, cat releases a jet of urine against surface or object.
Agonistic	Threat	Lion snaps teeth or swipes paw at conspecific, without making contact. Lion growls or hisses at conspecific, might be accompanied by movement towards the other individual.
	Chase	Animal propels itself forward into other individual's direction with the target animal fleeing and showing signs of fear.
	Hurt	Lion snaps teeth or swipes forepaw at conspecific, makes contact and possibly hurts the other.
	Fight	Two or more individuals engage in physical combat with each other.
	Fear	Individual actively avoids, flees or hides from conspecific, tucks tail under the body or trembles.
Exploratory	Sniff	Individual smells surface or object by inhaling air through the nose.
	Dig	Cat breaks up or moves substrate around with its paws.
	Flehmen	Cat makes a grimacing facial expression, where the mouth is open, upper lip is elevated, and tongue may protrude out of the mouth.
Maintenance	Groom	Individual cleans itself by licking, biting or chewing the fur on its body. May also include the licking of a front paw and wiping it over one's head.
	Yawn	Individual opens mouth widely, all teeth exposed, head moved upwards.

Table 3. State behaviour ethogram.

Behaviour	Activity	Description
Inactive	Lying	Animal is lying, eyes open or closed.
	Sitting	Individual is sitting down by having the forelimbs extended and the torso erect.
Active	Standing	Individual is standing with all four limbs extended.
	Walking	Individual is slowly walking forwards or backwards.
	Trotting	Individual is moving faster than walking in a trotting motion.
	Running	Individual is moving fast in a galloping motion.
Feeding	Feeding	Individual is actively manipulating food by licking, chewing and swallowing.
Pacing	Pacing	Individual is moving repetitively along the same path.

Methods

Subjects and husbandry

Four prides kept in four different zoos were included in this study. Two prides were kept on a high frequency feeding regime (HF) and received separate pieces of cow or horse meat on four to five occasions per week. The other two prides were kept on a low frequency feeding regime (LF) with one feeding of a whole carcass of cow or horse per week. Pride sizes, sex composition, average age of the animals and exhibit sizes of the four prides are summarized in Table 1. All 31 lions in this study were born and raised in captivity. Small cubs (0–1 years old) were excluded from the study.

Behavioural observations

Two ethograms were used: one included 19 behaviours clustered into five event behaviour categories (Table 2), the other included eight activity states clustered into four state behaviour categories

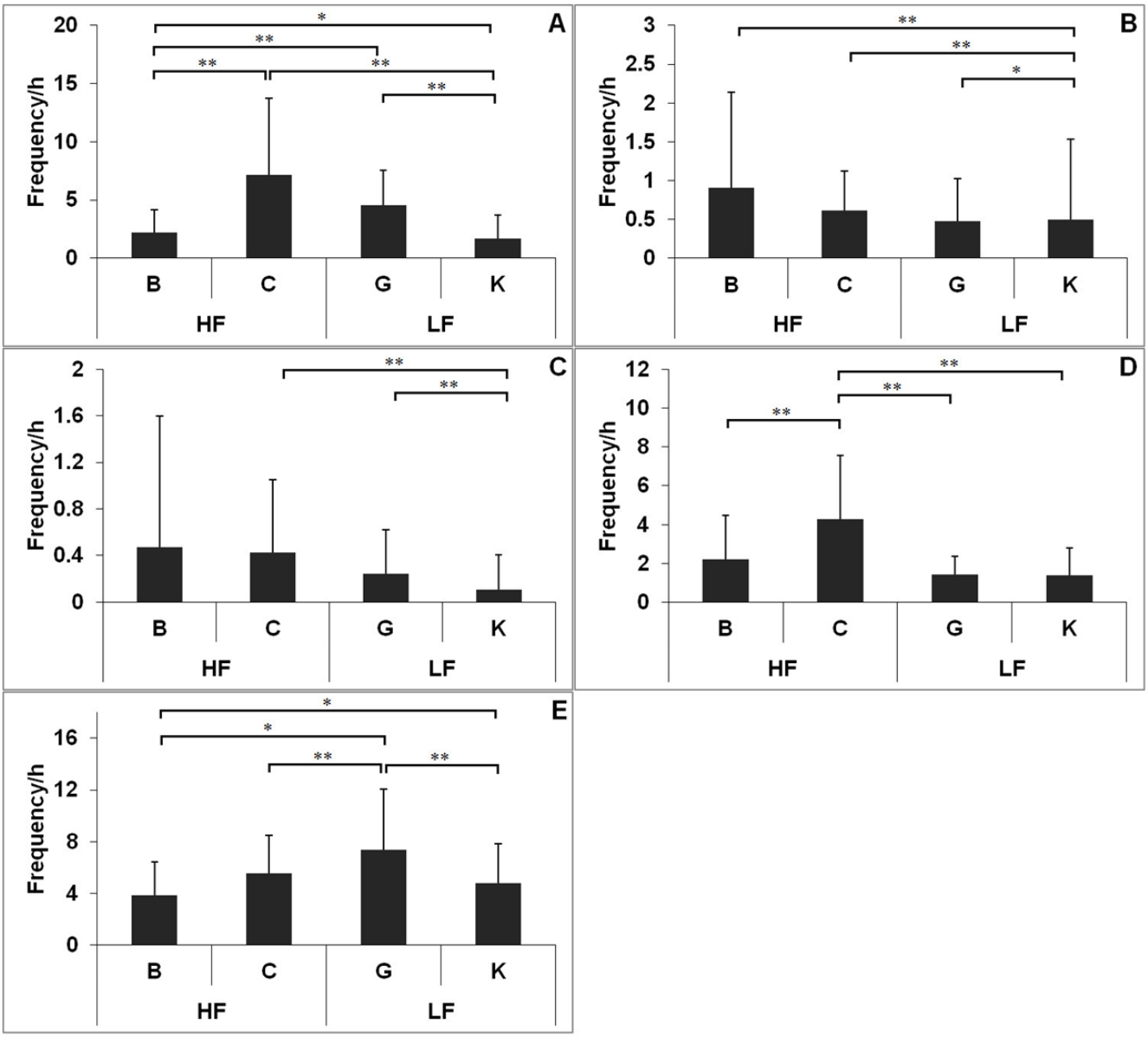

Figure 1. Frequency per hour of (A) social, (B) marking, (C) agonistic, (D) exploratory and (E) maintenance behaviours of the prides kept on high frequency feeding (HF) and low frequency feeding (LF). (B = Borås, C = Copenhagen, G = Givskud, K = Kolmården). Asterisks indicate $p<0.05$ (*) and $p<0.01$ (**), respectively.

(Table 3). Event behaviours and state behaviours, as well as the corresponding categories, were selected according to the standardized ethogram for Felidae by Stanton et al. (2015).

Event behaviours were recorded by behaviour sampling, whereby each occurrence of a particular behaviour is recorded for the whole group; state behaviours were recorded by instantaneous scan sampling at one-minute intervals (Altmann 1974). Data collection lasted 3 hours per day and took place between 4 pm and 8 pm. Each pride was observed for 24 consecutive days resulting in 288 hours of observation time for all four prides combined. All observations were performed by the same person (Nina Höttges), thus inter-observer reliability was not an issue. The four prides were observed from May until October 2016. All observations were made on the outdoor exhibits.

The protocol and procedures employed were ethically reviewed and approved by the Swedish Board of Agriculture (Jordbruksverket) and in accordance with EU Directive 2010/63.

Data analysis

All event behaviour data were combined according to behaviour category and normalised according to number of animals observed. Event behaviour data are presented as average frequency per hour per animal. All state behaviour data were combined according to activity category, normalised according to number of observed animals and presented as percentage of scans.

As the data were not normally distributed, non-parametric tests were used. Comparisons of behaviour or activity across prides and feeding regimes were conducted with the Kruskal-Wallis test, followed by pairwise Mann-Whitney U-tests for independent samples. To account for the problem of multiple comparisons, Bonferroni corrections were used where appropriate. Values are reported as means ±SD. The α-level was set at 0.05.

Results

Event behaviours

Among the five event behaviour categories considered in this study, maintenance behaviours were the most frequent, with on average 5.41±3.67 occurrences per hour in all four zoos combined, followed by social behaviours (3.8±4.31 times/h). Exploratory behaviour was recorded on average 2.26±2.39 times/h. Least frequent were marking behaviours and agonistic behaviours with on average 0.63±0.9 and 0.31±0.7 times/h, respectively.

Matthias Laska; e-mail: malas@ifm.liu.se Social behaviour

Social behaviour differed significantly between the four prides (Kruskal-Wallis: H=69.8; p<0.01). The Kolmården pride displayed significantly less social interactions than the lions in the other three zoos (K: Kolmården; B: Borås; C: Copenhagen; G: Givskud) (Mann-Whitney [K vs. B]: U=840.5; p<0.03; [K vs. C]: U=780.5; p<0.01; [K vs. G]: U=840.5; p<0.01). Furthermore, the lions in Borås were significantly less socially active than the lions in Copenhagen and in Givskud (Mann-Whitney [B vs. C]: U=986; p<0.01; [B vs. G]: U=1159.5; p<0.01) (Figure 1A). Social behaviours occurred more

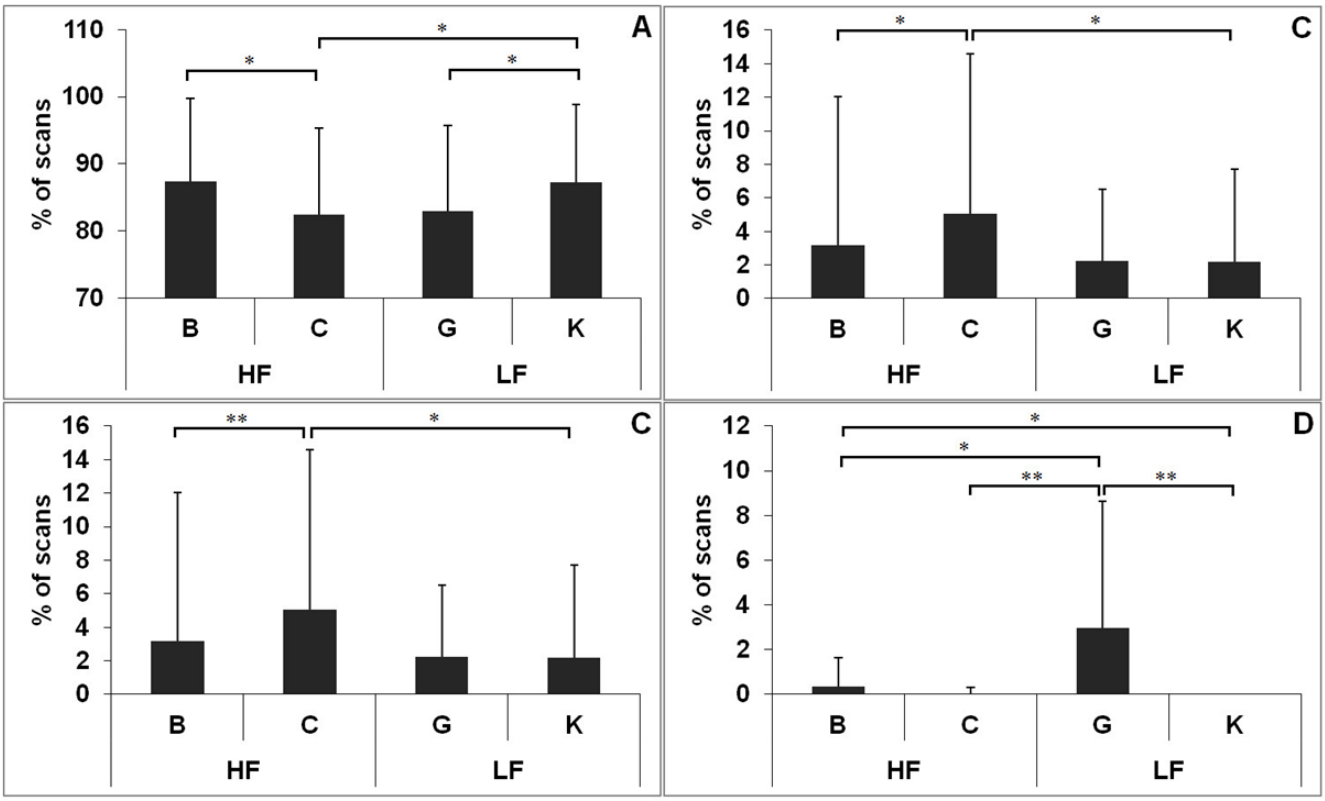

Figure 2. Percentage of scans spent with (A) inactive, (B) active, (C) feeding and (D) pacing activity of the prides kept on high frequency feeding (HF) and low frequency feeding (LF). (B = Borås, C = Copenhagen, G = Givskud, K = Kolmården). Asterisks indicate p<0.05 (*) and p<0.01 (**), respectively.

Table 4. Comparison of activity and behaviour categories on feeding and fasting days clustered for all four prides. Asterisks indicate p<0.05 (*) and p<0.01 (**), respectively.

Category	Feeding days	Fasting days	U	p
Social	2.77 ± 2.91	4.35 ± 4.81	6474	0.009**
Marking	0.54 ± 0.88	0.67 ± 0.91	7246	0.175
Agonistic	0.46 ± 1.0	0.23 ± 0.45	7094.5	0.072
Exploratory	2.45 ± 2.53	2.15 ± 2.32	7754	0.621
Maintenance	4.13 ± 2.9	6.08 ± 3.86	5278.5	0.000**
Inactive	83.13 ± 12.26	85.65 ± 11.56	7300	0.505
Active	10.07 ± 8.15	11.22 ± 9.48	6722.5	0.097
Feeding	6.74 ± 8.76	1.99 ± 4.71	4469	0.000**
Pacing	0.05 ± 0.91	1.14 ± 3.67	6478	0.001**

frequently in HF prides with 4.68±3.52 times/h as compared to LF prides with 3.1±2.05 times/h. This difference, however, was not statistically significant (Mann-Whitney: U=8060.5; p=0.19).

Marking behaviour

Marking behaviour differed significantly between the four prides (Kruskal-Wallis: H=17.1; p<0.01). The frequency of marking behaviour of the Kolmården lions was significantly lower compared to the frequency of marking behaviour of the other prides (Mann-Whitney [K vs. B]: U=1767; p=0.01; [K vs. C]: U=1184; p<0.01; [K vs. G]: U=1772; p<0.01) (Figure 1B). Marking behaviours were significantly more frequent for lions in HF prides (0.76±0.2 times/h) than for lions in LF prides (0.49±0.01 times/h) (Mann-Whitney: U=6839.5; p<0.01).

Agonistic behaviour

Agonistic behaviour differed significantly between the four prides (Kruskal-Wallis: H=13.18; p<0.01). Lions in Givskud and Copenhagen showed significantly more agonistic behaviour compared to the lions in Kolmården (Mann-Whitney [G vs. K]: U=1806.5; p<0.01; [C vs. K]: U=1409; p<0.01) (see Figure 1C). Lions on HF feeding engaged significantly more often in agonistic behaviours with 0.45±0.03 times/h compared to lions on LF feeding with 0.17±0.09 times/h (Mann-Whitney: U=7821.5; p=0.05).

Exploratory behaviour

Exploratory behaviour differed significantly between the four prides (Kruskal-Wallis: H=39.7; p<0.01). Exploratory behaviour was significantly more frequent for the lions in Copenhagen compared to the lions in Borås (Mann-Whitney: U=1208; p<0.01). Furthermore, exploratory behaviour was significantly more frequent for the lions in Copenhagen when compared to the lions in Givskud and Kolmården (Mann-Whitney [C vs. G]: U=935; p<0.01; [C vs. K]: U=868; p<0.01) (Figure 1D). Exploratory behaviours were

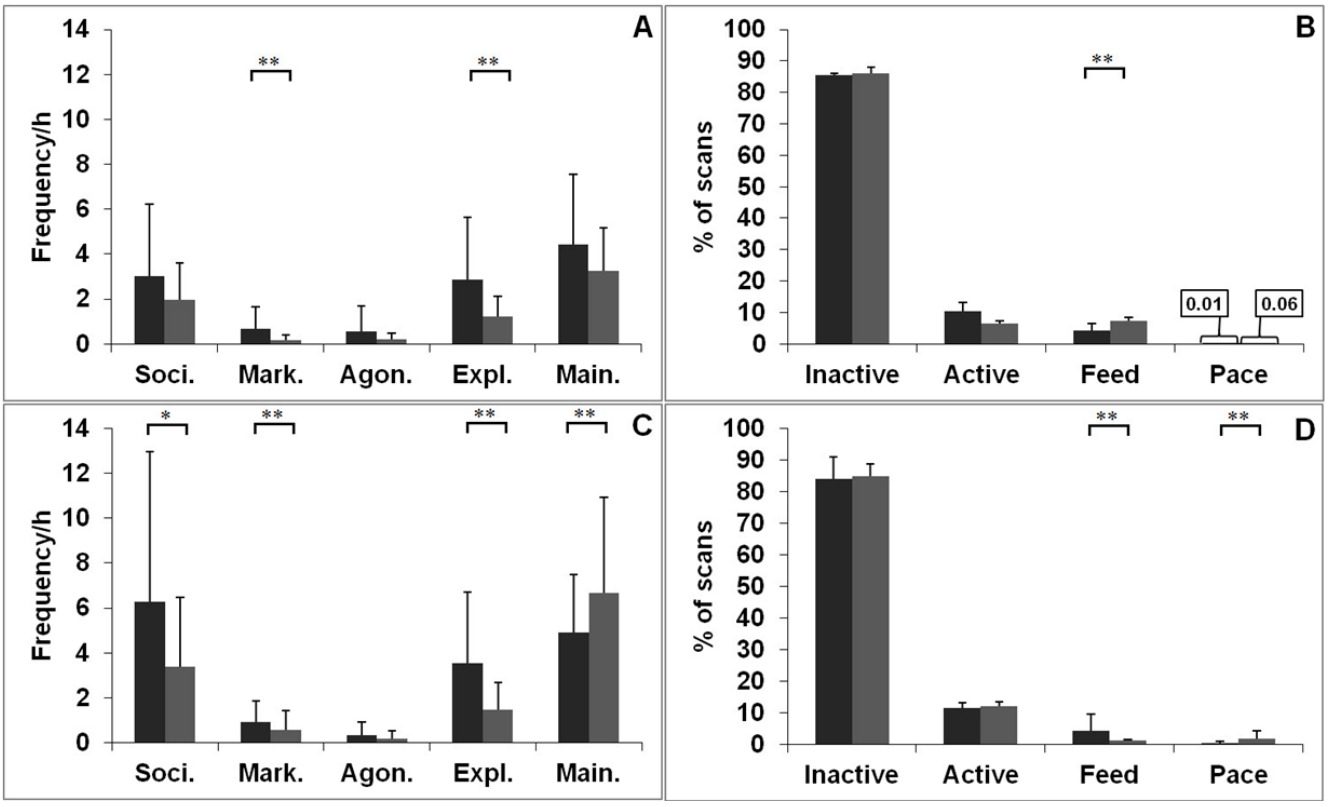

Figure 3. Behaviour categories (frequency/h) and activity categories (% of scans) for prides kept on high frequency feeding (dark grey) and prides kept on low frequency feeding (light grey). A and B represent data from feeding days, C and D represent data from fasting days. Asterisks indicate p<0.05 (*) and p<0.01 (**), respectively.
(Soci. = Social; Mark. = Marking; Agon. = Agonistic; Expl. = Exploratory; Main. = Maintenance)

significantly more frequent for lions on HF feeding (3.23±1.47 times/h) compared to lions on LF feeding (1.42±0.02 times/h) (Mann-Whitney: U=6062; p<0.01).

Maintenance behaviour

Maintenance behaviour differed significantly between the four prides (Kruskal-Wallis: H=35.58; p<0.01). Maintenance behaviours were significantly more frequent for the lions in Givskud in comparison to the other prides (Mann-Whitney: [G vs. B]: U=1067; p<0.01; [G vs. C]: U=1585; p=0.01; [G vs. K]: U=1457; p<0.01). Furthermore, maintenance behaviour was significantly less frequent in the Borås pride compared to the Copenhagen pride (Mann-Whitney: U=1368; p<0.01) (see Figure 1E). Maintenance behaviours were significantly less frequent for lions on HF feeding with 4.69±1.2 times/h compared to lions on LF feeding with 6.08±1.81 times/h (Mann-Whitney: U=6940; p<0.01).

State behaviours

Among the four state behaviour categories considered in this study, inactivity was by far the most frequently observed with 85.4±2.4% of scans on average in all four zoos combined, followed by active behaviour (10.7±1.3% of scans). Feeding accounted for 3.1±1.3% of the scans and least often recorded was pacing activity with 0.8±1.3% of the scans.

Inactivity

The level of inactivity differed significantly between the four prides (Kruskal-Wallis: H=7.41; p<0.01). The lions in Borås were significantly more inactive compared to the lions in Copenhagen (Mann-Whitney: U=1533.5; p=0.02). The Kolmården pride was significantly more inactive compared to the lions in Copenhagen and Givskud (Mann-Whitney: [K vs. C]: U=1520.5; p=0.02; [K vs. G]: U=1880; p=0.02) (Figure 2A). The lions on HF feeding and the lions on LF feeding spent a similar proportion of time with inactivity (84.88±3.56% of the scans; 85.11±3.01% of the scans, respectively) and thus did not differ significantly from each other in this category (Mann-Whitney: U=8782; p=0.94).

Activity

The proportion of time spent active did not differ significantly between the four prides (Kruskal-Wallis: H=69.8; p>0.05). On average, lions on HF feeding as well as LF feeding spent similar proportions of time with activity (10.8±2.45% of the scans; 11.19±0.87% of the scans, respectively) (Figure 2B) and thus did not differ significantly from each other in this category (Mann-Whitney: U=8702; p=0.84).

Feeding

The proportion of time spent feeding differed significantly between the four prides (Kruskal-Wallis: H=10.11; p=0.02). The lions in Copenhagen spent significantly more time feeding compared to the lions in Borås (Mann-Whitney: U=1533; p<0.01) (Figure 2C). On average, lions on HF feeding spent more time feeding (4.12±1.31% of the scans) than lions on LF feeding (2.21±0.04% of the scans). This difference, however, was not statistically significant (Mann-Whitney: U=8530.5; p=0.55).

Pacing

The proportion of pacing differed significantly between the four prides (Kruskal-Wallis: H=71.21; p<0.01). Pacing was significantly higher for the lions in Givskud compared to the prides in the other three zoos (Mann-Whitney: [G vs. B]: U=4036.5; p=0.01; [G vs. C]: U=1205; p<0.01; [G vs. K]: U=1326; p<0.01). The Borås pride paced significantly more often than the lions in Kolmården (Mann-Whitney: U=2108; p=0.01) (Figure 2D).

Feeding and fasting days

Lions on both feeding regimes showed increased levels of social, marking, exploratory and maintenance behaviours during fasting days compared to feeding days. Agonistic behaviours were more frequent during feeding days compared to fasting days. On average the four prides showed higher proportions of time spent with feeding and inactivity during feeding days and higher levels of pacing and activity during fasting days (Table 4).

Feeding days

During feeding days, the lions kept on HF feeding showed significantly more marking and exploratory behaviour compared to the lions on LF feeding (Mann-Whitney: [Marking]: U=490.5; p<0.01; [Exploratory]: U=551; p=0.03). No significant differences between feeding regimes were found for the three remaining behaviour categories (Mann-Whitney: [Social]: U=683; p=0.32; [Agonistic]: U=755.5; p=0.71; [Maintenance]: U=630; p=0.14) (Figure 3A).

During feeding days, lions kept on LF feeding spent significantly more time feeding compared to lions kept on HF feeding (Mann-Whitney: U=432.5; p<0.01). No significant differences between feeding regimes were found for the four remaining activity categories (Mann-Whitney: [Inactivity]: U=687; p=0.8; [Pacing]: U=710; p=0.94; [Activity]: U=574; p=0.17) (Figure 3B).

Fasting days

During fasting days, lions on HF feeding showed significantly more social, exploratory and marking behaviours and significantly fewer maintenance behaviours compared to lions on LF feeding (Mann-Whitney: [Social]: U=2649.5; p=0.02; [Exploratory]: U=2113; p<0.01; [Marking]: U=2416; p<0.01; [Maintenance]: U=2477; p<0.01). Agonistic behaviours did not differ significantly between feeding regimes ([Agonistic]: U=3017.5; p=0.14) (Figure 3C).

Lions kept on HF feeding spent significantly less time pacing and significantly more time feeding during fasting days compared to feeding days (Mann-Whitney: [Pacing]: U=3045; p<0.01; [Feeding]: U=432.5; p<0.01). No significant differences between fasting and feeding days were found for the two remaining activity categories (Mann-Whitney: [Active]: U=3767.5; p=0.99; [Inactive]: U=687; p=0.8) (Figure 3D).

Discussion

We found that agonistic, exploratory and marking behaviours, as well as feeding activity of captive lions, were markedly affected by feeding regime. These behaviours and activities were more frequent for lions on HF feeding than for lions on LF feeding. On both feeding regimes, agonistic encounters as well as time spent feeding and time spent inactive were more frequent during feeding days than during fasting days. Lions on both feeding regimes were more active and paced more often during fasting days. Further, lions on both feeding regimes engaged more frequently in exploratory, maintenance, marking and social behaviours during fasting days.

Event behaviours

Social and agonistic behaviour

Social as well as agonistic behaviours were significantly more frequent for lions on HF feeding compared to their conspecifics on LF feeding. Feeding is considered the 'most common context for aggressive competition in lions' (Packer et al. 2001) and therefore it seems likely that alliances are established or maintained during communal feeding. If social discrepancies are solved during communal feeding, lions on HF feeding, who were fed with separate pieces of meat, must resolve their social tensions outside

of the feeding context. This may explain the higher level of social and agonistic interactions found in HF feeding in the present study. For some social living species, such as bush dogs, carcass feeding is considered to benefit the group cohesion, which suggests that lions too might benefit from whole carcass feeding (Macdonald 1996).

For lions on both feeding regimes, affiliative social behaviours were less frequent on feeding days compared to fasting days. Social gestures help create group cohesion and are not only used to strengthen individual bonds, but also to initiate common activity (Schaller 1972; Packer and Pusey 1997). Lions in the wild have been reported to increasingly display social behaviour before setting out to hunt and immediately after agonistic encounters (Schaller 1972; Packer et al. 2001; Matoba et al. 2013). The increased social interactions during fasting days can thus be interpreted as the disposition to tolerate each other and/or to cooperate in food acquisition as well as the reestablishment of social bonds after feeding.

For lions on both feeding regimes, agonistic behaviours were more frequent on feeding days than fasting days. This finding is not surprising as the act of feeding is the most common situation for agonistic encounters to occur in lions (Packer et al. 2001). However, agonistic behaviours were higher in HF prides compared to LF prides. This indicates that carcass feeding may reduce agonistic encounters more efficiently than presenting meat to individuals separately.

Sociality among lions depends primarily on genetic relatedness and age of the pride members (Schaller 1972; Packer and Pusey 1997; Packer et al. 2001). Social play and affectionate attention are behaviours that lion cubs frequently engage in or receive from other pride members (Schaller 1972). The presence of cubs may therefore skew the data towards a higher frequency of social interactions. The Copenhagen pride had the lowest mean age (2.6 years) and showed the highest frequency of social behaviours (7.17 times/h), followed by the Givskud pride (average of 4.9 years; 4.55 times/h) and the pride in Borås (average of 10.3 years; 2.2 times/h). Surprisingly, the Kolmården pride was the second youngest group (average of 4.2 years) but showed the lowest frequency of social behaviours (1.65 times/h). Three confounding factors may have contributed to this finding:

1. Behaviours directed towards or received from small cubs were excluded from this study. As lionesses raise young collaboratively, social behaviours of the Kolmården pride were focused on the present small cubs rather than other adults (Packer and Pusey 1997).

2. Much of the social play behaviour took place in dense vegetation and could not be recorded.

3. As lion mothers tend to separate from the pride, the level of social behaviour she directed towards other pride members was lower than it would have been without cubs or with older, more independent cubs.

Therefore, we cannot exclude the possibility that the frequency of social behaviours did not primarily depend on feeding regime, but on group composition, reproductive state and average age of the pride.

Furthermore, social interactions of captive lions are known to adapt to limited availability of space (Abell et al. 2013). Transferring lions to a bigger enclosure has been found to result in a decrease of mainly agonistic and to a lesser extent social behaviour (Clarey and Farnsworth 1983). In the present study, the prides held in the smaller exhibits (2150m², 703m²) were also the prides fed both on HF feeding, whereas the prides on LF feeding inhabited relatively large exhibits (50,000m², 25,000m²). The elevated frequencies of social and agonistic behaviours that we observed in lions on HF feeding may thus have been influenced by limited enclosure size. This notion is further supported by Altman et al. (2005) who observed no increase in agonistic or social behaviour when a lion pride on HF feeding was switched to LF feeding.

Marking

Marking behaviour was significantly more frequent for lions on HF feeding (0.76 times/h) than for lions on LF feeding (0.49 times/h). Urine spraying has been reported to regularly occur following agonistic encounters (Schaller 1972; McComb et al. 1994). In the present study the frequency of marking behaviour corresponded to the frequency of agonistic behaviour (see above Social and agonistic behaviour). Lions on HF feeding engaged more frequently in agonistic encounters, which were accompanied by marking behaviours. Accordingly, in LF prides, where agonistic behaviours occurred less often, marking behaviours were less frequent.

Exploratory

Exploratory behaviours were significantly more frequent for lions on HF feeding (3.23 times/h) than for lions on LF feeding (1.42 times/h). This seems counterintuitive, as a longer period between feedings and the hunger resulting from several consecutive fasting days should lead to elevated foraging behaviours such as exploration (Horat et al. 1994; Hansen et al. 2015). Leyhausen and Tonkin (1979) reported that exploratory behaviour in small cats is dependent on hunger: less food given during feeding time causes more exploration. Thus, it is possible that the smaller amount of food given to lions on HF feeding did not lead to complete satiation. Elliott et al. (1977) found that the level of satiation, measured as the amount of food consumed, correlated significantly with the time delay until the next active search for prey was initiated. Accordingly, it is possible that lions on HF feeding did not reach a level of satiety that kept them occupied with digestion until the next feeding. This could also explain the higher frequencies of exploratory behaviour during fasting days for lions on both feeding regimes.

Maintenance

Lions on LF feeding engaged more frequently in maintenance behaviours (6.08 times/h) than lions on HF feeding (4.69 times/h). However, frequencies of maintenance behaviour were more similar for lions on different feeding regimes than for lions on the same feeding regime. This suggests that the feeding regime has no systematic impact on the average frequency of maintenance behaviour in captive lions. For lions on HF feeding, maintenance behaviours were similarly frequent on feeding (4.42/h) and fasting days (4.9/h), whereas lions on LF feeding engaged less frequently in maintenance behaviours during feeding days (3.25/h) compared to fasting days (6.68/h). The lower levels of maintenance behaviour expressed by lions on LF feeding during feeding days indicates drowsiness as a result of satiety after feeding. The rather constant and higher levels of maintenance behaviour in HF prides, on the other hand, imply the lack of satiety and drowsiness.

Inactivity and activity

On average, the lions on both feeding regimes spent a similar proportion of time being inactive (84.88% of the scans for lions on HF feeding and 85.11% of the scans for lions on LF feeding) and active (10.8% of the scans for lions on HF feeding and 11.19% of the scans for lions on LF feeding).

For a variety of species increasing hunger results in increasing activity (Horat et al. 1994; Walker et al. 1999). Wild-living lions have been found to display a negative correlation between the amount of food ingested and distance travelled during the 24 hours after feeding (Van Orsdol 1984). Further, Elliott et al. (1977) found a positive correlation between the amount of food ingested and time until lions started foraging again. Accordingly, lions on both feeding regimes were more inactive when satiated during

feeding days and more active when food-deprived during fasting days. As each lion held on HF feeding ingested 5–6 kg per feeding, their activity during feeding and fasting days was high (10.3% and 12.1%, respectively), indicating a lack of satiety. In contrast, the lions on LF feeding each ingested approximately 33.3kg of meat and were less active during feeding day and fasting day 1 due to satiety (6.5% and 8.74%, respectively).

A high proportion of time being inactive can precede feeding and may thus be counted together with stereotypic pacing or other abnormal behaviours as food-anticipatory activity (Bloomsmith and Lambeth 1995; Waitt and Buchanan-Smith 2001; Mallapur and Chellam 2002). For the lions in the present study, the inactivity levels did not vary across fasting days and were similar for lions on HF feeding and lions on LF feeding. However, it would be interesting to conduct further studies that focus on the time before feeding to assess possible differences in food-anticipatory behaviour in lions on HF feeding and those on LF feeding.

Feed

Lions on HF feeding spent on average more time with feeding (4.12% of the scans) than lions on LF feeding (2.21% of the scans), as the former received fresh food 4–5 days a week, which resulted in a continuous supply of food scraps in the exhibit. The proportion of time spent feeding was almost evenly distributed between feeding and fasting days in HF prides (4.29% on feeding days and 4.12% on fasting days). In contrast, lions on LF feeding ate mostly during feeding days (7.38% of the scans) and very little during fasting days (1.2% of the scans). Our data show that the lions on LF feeding, which were provided with carcasses, occupied themselves with the food for at least two days. This resembles findings in the wild, where lions were observed at carcasses for up to two days (Eloff 1984). However, the lions on HF feeding spent a considerable amount of time feeding given that they were usually finished feeding within an hour after they received their meat. However, these lions engaged in gnawing on the leftover bones, which is unusual for wild-living lions (Van Valkenburgh 1996).

The food intake of a wild-living lion can be as high as 25kg in one sitting (Lindburg 1988). Schaller (1972) even reported that two free-ranging male lions each ingested an estimated 43kg of meat. The average daily food intake ranged from 4.6kg to 6.4kg in the Karongwe game reserve (Lehmann et al. 2008) and 4.7kg for female lions to 7.2kg for male lions in the Kalahari Desert (Eloff 1984). Although fed more frequently, lions on HF feeding had a daily food intake of merely 3kg whereas lions on LF feeding had an average daily food intake of 4.76kg. Although lions in captivity need a lower energy intake than their wild-living conspecifics as the former do not have to hunt, the effect of both satiation and satiety has to be considered when adapting a feeding regime.

Pacing

On average, the lions on LF feeding paced during 1.49% of the scans and thus significantly more than the lions on HF feeding who paced during 0.19% of the scans. However, while the proportion of time spent pacing in Givskud was significantly higher than the proportion of time spent pacing in the other zoos, the lions in Kolmården, which were fed on LF feeding, too, did not pace at all. It is thus apparent that other factors than feeding regime have influenced pacing behaviour in the two LF prides.

Pacing was more frequent on fasting days compared to feeding days for lions on both feeding regimes. This pattern was also described by Lyons et al. (1997) who found that felids fed every third day paced more during fasting than feeding days. The authors also found that lions fed daily did not pace as much as lions fed every third day. This resembles our finding that lions on HF feeding paced less during fasting days than lions on LF feeding during fasting days.

Conclusions

The results of the present study show that captive lions maintained on a high frequency feeding regime displayed elevated levels of agonistic and exploratory behaviour as well as elevated levels of activity which can be explained by a lack of satiety. In contrast, lions kept on a low frequency feeding regime displayed low levels of maintenance behaviour as well as low levels of activity during the feeding day and the first fasting day, which indicates drowsiness due to satiety. Furthermore, lions on both feeding regimes showed higher levels of agonistic behaviours and higher levels of inactivity during feeding days compared to fasting days. To promote good welfare and more naturalistic behaviour of captive lions we suggest shifting feeding regimes away from high frequency feeding and towards low frequency feeding.

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