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Using longitudinal data to evaluate the behavioural impact of a switch to carcass feeding on an Asiatic lion *Panthera leo persica*

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Abstract

Replicating species-specific feeding behaviours in captive carnivores has presented a challenge for zoological collections. Many studies highlight the benefits of a naturalistic feeding programme on the physical health and psychological well-being of individuals, with the provision of carcasses found to increase appetite and active behaviours and reduce stereotypic pacing. Whilst some studies have documented the behavioural impact of a naturalistic dietary change, information is often lacking on the long-term effect of a transition towards a more species appropriate diet. This paper presents results from a long-term study of a female Asiatic lion *Panthera leo persica* at Chester Zoo. Behavioural data were collected before and shortly after a change in diet regime, from daily pre-processed joints of meat to whole calf carcass followed by fast days. To assess the long-term behavioural impact of this management intervention, data were also collected 12 months after carcass feeds were introduced. The results show a significant reduction in pacing behaviour 12 months after the change in diet. Resting behaviour was also affected by diet change, with a significant increase in resting reported 12 months after a carcass feeding regime was introduced. Additionally, an alteration in feeding behaviour was recorded, with a significant increase in average time spent feeding both shortly after and 12 months after the carcass feed regime was implemented. Here, this paper shows the value of using longitudinal behavioural data as a tool to evaluate the effectiveness of diet changes and demonstrates how this information can facilitate the implementation of evidence-based management decisions.

Background

Along with health status, the replication of wild-type behaviours by species in captivity is regarded as one of the many indicators of positive welfare (Veasey et al. 1996; Veasey 2006). Therefore, many zoological collections strive to increase species-specific behaviour in their animals; either through the provision of enrichment (Tarou and Bashaw 2007), the implementation of natural feeding regimes (Gilbert-Norton et al. 2009), or modifications to enclosure design (Lukas et al. 2003).

Carnivores are a taxon of particular concern, especially those that are naturally wide-ranging, as they commonly exhibit higher incidences of pacing behaviour in captivity (Clubb and Mason 2003). Many zoos have worked to significantly improve carnivore husbandry, with a focus on offering species-appropriate diets (Bauman et al. 2010).

Previously, the desire to provide individuals with adequate nutrition and a balanced diet often resulted in failure to offer food items which fulfilled other non-nutritive requirements. It is now known that these components are essential in replicating species-specific behaviours and maintaining

physiological and psychological well-being. Fitch and Fagan (1982) highlighted cheetahs *Acinonyx jubatus* as an example, reporting that individuals fed a soft, pre-processed diet, which was historically the most common diet across collections, exhibited symptoms of focal palatine erosion and dental deformities due to the lack of appropriate dietary texture. This has been found in other captive species, with elephants *Elephas* and lagomorphs *Lagomorpha* presenting malocclusion issues stemming from a lack of abrasive tissue in their diets (Lindburg 1988). Whitehouse-Tedd et al. (2015) reported that feeding ribs and long limbs to captive cheetahs reduced the occurrence of diarrhoea and vomiting whilst the provision of muscle meat at least once a week reduced the prevalence of individuals suffering from chronic gastritis or other forms of non-specific gastrointestinal disease.

It is important to note that providing species with inadequate diets does not just affect the animals' physiology. Failure to express species-specific hunting behaviour in large carnivores can lead to appetite frustration, which can result in a higher proportion of stereotypic pacing (Carlstead and Seidensticker 1991). Wild carnivores spend many hours crushing bones, tearing flesh and picking the fur off carcasses (MacDonald 1984); something which cannot be replicated if pre-processed meat joints are fed in captivity. As a consequence, extending the length of feeding in captivity by providing carcasses, allows individuals to engage in these species-specific feeding bouts.

In response to these outlined issues, many collections have changed the diet of their carnivores to include more abrasive components such as bone and cartilage (Whitehouse-Tedd et al. 2015). Subsequently, numerous studies have highlighted the positive welfare benefits of a more naturalistic feeding regime (Bond and Lindburg 1990). McPhee (2002) documented an off-exhibit decrease in stereotypic behaviour for nine large felids following the provision of intact carcasses and Ruskell et al. (2015) highlighted that the presentation of a carcass on a bungee cord significantly reduced pacing behaviour in both Bengal tigers *Panthera tigris tigris* and cougars *Felis concolor*.

However, many studies have restricted data collection to a short period following the transition to a more naturalistic diet. Mason et al. (2013) suggest that the impact of a management change on behaviour may not always be immediately apparent, as many captive animals exhibit a reduced behavioural flexibility, leaving them less able to cope with changes to their environment. In light of this, individuals may take much longer to adapt to husbandry and management changes, emphasising the importance of longitudinal behavioural monitoring (Mason et al. 2013).

The subject of the present study was highlighted as an individual that required increased monitoring, due to an observed increase in her levels of repetitive pacing behaviour. The initial aim of the behavioural project was to quantify her activity budget and report any potential triggers of pacing. In conjunction with behavioural monitoring, the diet of the whole group was evaluated, leading to a recommended transition towards a more species-appropriate feeding regime. The study developed a new aim, requiring continued behavioural monitoring in order to evaluate the short and longer-term impacts of carcass feeding on activity budget, whilst keeping a particular focus on pacing behaviour.

Action

The subject was a 9 year-old female Asiatic lion *Panthera leo persica* at Chester Zoo, UK. This individual was group-housed with one unrelated male and one related female, her full sister. The enclosure size totalled 2255m^2 which encompassed a multi-substrate outdoor exhibit, including grass and sand, a grass mound, living trees and shrubs, and an indoor den. The group had 24-hour access to the whole enclosure, except during keeper maintenance times and adverse weather conditions.

Table 1. Pre-defined ethogram of Asiatic lion behaviour.

Behaviour	Description
Alert	Highly responsive to stimuli. Looking around or focused in a specific direction.
Digging	Using paws to displace substrate.
Feeding	Ingestion of food item or liquid.
Excretion	Elimination of urine and faeces from body.
Grooming	Self-maintenance which includes rolling, stretching, licking, scratching and biting of own body.
Locomotion	Walking or running from one place to another. Does not include pacing.
Object interaction	Licking, scratching, rubbing or scent-marking an object within the enclosure.
Out of sight	The subject is not visible to the observer.
Pacing	Continuous walking back and forth in a repetitive way for at least three times.
Resting	Lying down, body motionless, note if eyes open or closed.
Sniffing	Brief inhalation of object, ground, or air during olfactory investigation.
Social interaction	Any form of interaction with a conspecific. Includes aggression, rubbing heads, courtship, allo-grooming, etc.
Vocalisation	Opening mouth and producing sound. May occur while solitary, at a conspecific, or at human(s).
Yawning	Opening mouth widely and exhaling.

Data were collected using instantaneous focal sampling at 30-sec intervals throughout a 60-min observation period per day. At each interval, behaviour was recorded using a pre-defined ethogram (Table 1). Inter-observer reliability tests were conducted and achieved over 90%, with each observer using these standardised methods. Data collection occurred between 0900 and 1700, with the collection schedule being randomised but balanced to ensure that all time periods across the day were observed equally. When multiple observation sessions occurred on the same day, an average was taken of these data. From this information, a daily activity budget was calculated, outlining the proportion of time the individual was engaging in each behaviour (Table 1). These data were then used for statistical analysis. Raw data were used to evaluate the impact that a change in feeding regime had on the amount of time spent feeding. Total observation time equated to 77 hours.

The data were collected during three conditions: 1. Pre-carcass regime: 11 days pre-diet change (29 Mar 2016 – 22 Apr 2016); 2. Post-carcass regime: 11 days shortly after carcass feeding regime had started (04 Jun 2016 –17 May 2016); and 3. 12 months post-carcass regime: 11 days of data collected 12 months following the diet change (03 May 2017 – 17 May 2017).

The subject remained in a consistent social grouping, with no major management changes during the data collection window. The diet of the subject pre and post change is outlined (Table 2) and feeding times were randomised across the day by keeping staff. Once the carcass feeding regime was implemented, some descriptive interpretation was installed around the exhibit for visitors, highlighting the natural feeding behaviours of wild lions and explaining how this was being replicated in a captive setting.

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Table 2. Weekly diet of subject throughout study.

Pre-carcass regime	Mon	Tues	Wed	Thurs	Fri	Sat	Sun
Beef joint (3 kg)	Yes	Yes	Yes	Yes		Yes	Yes
Whole chicken (1.5–2 kg)					Yes		
Post-carcass regime	Mon	Tues	Wed	Thurs	Fri	Sat	Sun
Calf carcass (20–25 kg)			Yes			Yes (1/3)	Yes (1/3)
Calf leg (~5 kg)	Yes						
Whole chicken (2 kg)					Yes		

Additionally, this study investigated the influence of carcass feeding on the number of feeding bouts observed. A feeding bout was defined as when the study individual was engaging in feeding behaviour then stopped feeding for over one minute. Raw data were used to calculate the average amount of time spent feeding, when food was available within the exhibit. For the 'pre-carcass regime' condition this was every day. However, once the carcass feeding regime was implemented (Table 2) no food was offered on two days per week, acting as a 'fast day' for the study individual.

As each response variable was found to have a normal distribution (Shapiro-Wilks test: Pacing: w=0.9243, P=0.2104, Resting: w=0.9675, P=0.3151, Feeding: w=0.9527, P=0.1813), one-way ANOVAs with appropriate Tukey post-hoc tests were conducted to compare the effect of feeding regime (pre-carcass regime, post-carcass regime and 12 months post-carcass regime) on the time spent engaging in pacing, resting and feeding behaviour. All values are reported as means ± standard error.

Consequences

Pacing

Overall results revealed that carcass feeding significantly reduced the average time spent pacing (F=7.496, P=0.002). However, there was no significant decrease in the average time spent pacing from pre-carcass regime to post-carcass feeding regime (P=0.119) (Figure 1, graph (a)). In contrast, 12 months after the carcass feeding regime was implemented, levels of pacing had significantly reduced from 21% (±5.2%) to 0.1% (±0.07%) (P=0.001) (Figure 1a).

A reduction in pacing following a transition towards a more species-appropriate diet is a trend which has been observed in other studies (McPhee 2002; Altman et al. 2005), with Bashaw et al. (2003) highlighting that bone presentation reduced stereotypic pacing behaviour in both African lions *Panthera leo* and Sumatran tigers *Panthera tigris sumatrae*. In addition, Bashaw et al. (2003) reported that bone presentation had a sustained effect on

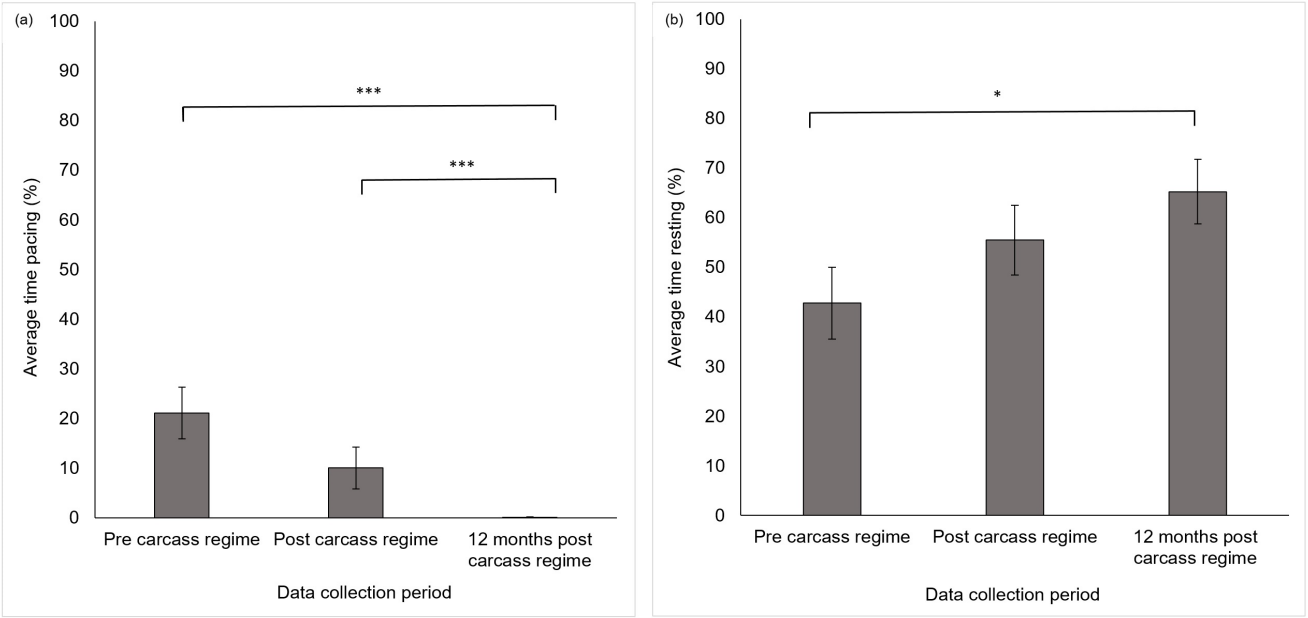

Figure 1. Average time study individual engaged in pacing behaviour (a) and resting behaviour (b) across the three data collection periods (***P≤0.001, **P≤0.01, *P≤0.05).

Table 3. Average number of feeding bouts and the average length of feeding bouts displayed by the study individual throughout each data collection period.

	Pre-carcass regime	Post-carcass regime	12 months post-carcass regime
Average bout length (mins)	6.2 (±1.1)	20.5 (±3.7)	20.6 (±4.01)
Average bout number	3.2 (±0.86)	2.7 (±0.88)	1.7 (±0.33)

behaviour, with reduced stereotypy observed for at least two days after implementation. The present study's long-term findings supplement the study by Bashaw et al. (2003), in which it was suggested that alternative feeding strategies can alter underlying activity patterns of individuals. The lack of immediate significant reduction in pacing in the weeks following the diet change is likely due to a lag in the subject adapting to the gorge and fast feeding routine. This result highlights the value of longer-term monitoring following husbandry and management changes.

Resting

Following the transition to carcass feeding, resting behaviour was found to significantly increase between data collection periods (F=3.580, P=0.038). Post-hoc analysis revealed that average time spent resting significantly increased from pre-carcass regime levels of 42.8% (±7.3%) to 65.2% (±6.5%) 12 months post-carcass feeding regime (P=0.029) (Figure 1b). High levels of inactivity are often reported as a common problem with large captive carnivores (Kistler et al. 2009). However, some argue that elevated levels of resting behaviour are more representative of a wild individual's activity budget as a naturalistic feeding pattern of gorging followed by fasting would encourage increased resting on gorge days (Clark 1987; Stander 1992). Additionally, a study into vigilance behaviour of social carnivores (Pangle and Holekamp 2010) reported that hyenas *Crocuta crocuta* were less vigilant when feeding on a high-quality food source such as a large carcass, than when consuming a low-quality food source. De Cuyper et al. (2018) further support this theory, reporting that wild carnivore inactivity levels are high due to individuals trying to reduce their hunting related activity as much as possible as an energy saving mechanism. Individuals achieve this by feeding on larger prey items less frequently.

Feeding

The feeding behaviour of the study individual was influenced by the change in husbandry regime, with carcass feeding having a significant influence on the length of feeding bouts (F=17.751, P<0.001).

The amount of time spent feeding per bout significantly increased from an average of 6.2 (±1.1) min before carcass feeding was introduced, to an average of 20.5 (±3.7) min shortly after carcass feeding was introduced (P=0.001) (Table 3). This was sustained 12 months later with feeding bouts continuing to average 20.6 (±4.0) min (P=0.001) (Table 3). Whilst bout length increased post carcass, no significant difference was observed in number of feeding bouts across the three data collection periods (F=2.92, P=0.088) (Table 3).

Furthermore, the average time spent feeding per observation session was calculated following the implementation of the carcass feeding regime (Figure 2). The results revealed that carcass feeding significantly influenced the amount of total time spent feeding by the study individual (F=8.37, P=0.004). Post-hoc analysis revealed a significant initial increase in total time spent feeding from pre-carcass regime to post-carcass feeding regime from an average of 16.37 min (±3.22) to 48.67 min (±11.7) (P=0.004) (Figure 2). Additionally, there was a significant increase in total time spent feeding from pre-carcass to 12 months post-carcass feeding regime (P=0.045) (Figure 2). The results highlight that the effect of providing a carcass on total time spent feeding was sustained, with no significant difference in time spent feeding found from immediately post-carcass regime to 12 months post-carcass regime (P=0.29) (Figure 2).

Increased feeding time was a trend also observed by Altman et al. (2005) who reported a significant increase in appetite-active behaviours following the implementation of a gorge and fast feeding schedule in African lions. Altman et al. (2005) further highlighted the nutritional benefits of a more naturalistic feeding regime with a reported significant increase in digestibility of food offered and significant decrease in metabolisable energy intake of their study individuals. Improving the nutritional status of lions also tackles obesity, a common problem often observed in captive carnivores (Clauss et al. 2010).

It could be argued that time spent feeding increased because the study individual was fed more (in weight) of food item following the implementation of carcass feeding. Whilst the carcasses did weigh more in total, the actual amount of meat offered was similar in weight to the joints provided in the pre-carcass feeding regime. This is due to the carcasses containing much more indigestible material such as bone and hide, than the pre-processed joints. The evidence highlighting the physiological and behavioural benefit of providing captive carnivores with abrasive tissue in their

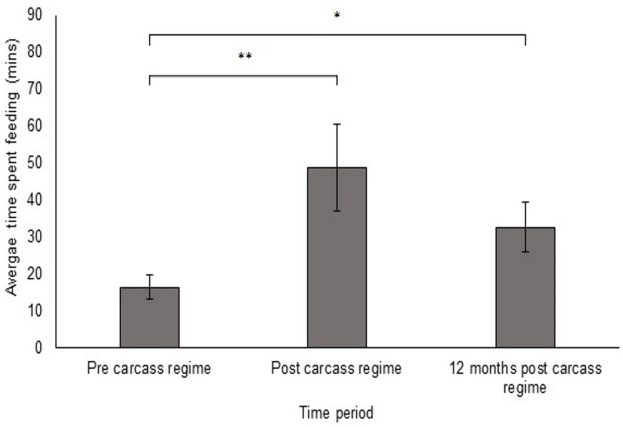

Figure 2. Average time spent feeding across the three data collection period (***P≤0.001, **P≤0.01, *P≤0.05).

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diet has already been presented and discussed in this study. In consequence, the increased feeding time observed in this study is further evidence that bones and other tissue, when provided, encourages and extends natural feeding behaviour of captive carnivores. The data also show the sustained effect that carcass feeding has on behaviour, with feeding times increasing and remaining consistent 12 months after implementation (Table 3). Throughout this study, the carcasses offered were of a consistent weight thus not biasing the length of time spent feeding. Further research directions should include an intake study to quantify exactly how much of the carcass is consumed, providing more precise values of meat offered. In addition, if the study were to be repeated, the authors would see value in conducting regular body condition scoring of individuals following a diet change, this is to achieve a physiological measure of the influence of carcass feeding. The study would also include the behavioural reactions of other members of the pride. Whilst this was not evaluated during the present study, anecdotally it was observed initially that the male was aggressive and protective over the presented carcasses, potentially as they were a high value resource. Once individuals settled into the regular routine of carcass feeding (Table 2), this behaviour was seen less frequently.

Some zoos have reported negative comments or attitudes from their visitors towards feeding full carcasses (Gaengler and Clum 2015). Whilst this was not evaluated during the present study, the keepers did not report any negative comments or questions regarding the use of carcasses from visitors.

It should be noted that this study was focused on a single subject: single animal case studies are useful for highlighting individual behavioural responses but further testing on other groups, across multiple institutions would provide more information, in particular when evaluating the influence of pride level dominance on carcass feeding. This study highlights the value of evaluating the diets of captive individuals, to ensure that not only their nutritional needs are being met, but the psychological and behavioural requirements of species are also taken into consideration. The results would especially benefit colleagues that may be feeding soft and pre-processed diets to captive carnivores.

Furthermore, the present results show a sustained influence on behaviour following the implementation of carcass feeding, with trends observed to be maintained or highlighted 12 months after the diet change. As previously discussed, captive animals are suggested to have a reduced behavioural flexibility (Mason et al. 2013). In consequence, it is suggested that longitudinal behavioural monitoring provides novel and robust information, allowing a comprehensive evaluation of the well-being of individuals in captive collections.

Conclusion

1. The implementation of a more naturalistic feeding schedule decreased pacing behaviour and increased species-specific resting behaviour in the study individual.
2. The presentation of carcasses instead of pre-processed joints of meat significantly increased the length of feeding time in the study individual.
3. Assessing the long-term impact of a modification in diet may reveal behavioural changes that were not immediately apparent, highlighting the value of longitudinal monitoring of individuals post management change.

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