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The behavioural effects of feeding lean meat vs whole rabbit carcasses to zoo jaguars *Panthera onca*

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Abstract

The challenge of carnivore feeding in zoos is to stimulate natural feeding behaviour without using live prey animals. The objective of this study was to investigate how two different feed types (lean beef and whole rabbits) affect the behaviour of zoo jaguars *Panthera onca* for the first six hours after feed presentation. Three socially housed jaguars at Parken Zoo, Sweden, were offered either lean beef or whole rabbits for 10 consecutive feeding days. Their behaviour during and after feeding was video-recorded and then compared between the two feed types. When analysing the frequency of different behaviours for six hours after feeding, results confirm that feeding behaviour occurred significantly more frequently when whole rabbits were fed, particularly during the first hour after feed presentation. However, even though feeding time increased by more than 300%, this represents a change of less than 1% in terms of the overall proportion of a 24-hour budget. Future studies might investigate the effect of feeding jaguars larger carcasses than rabbits, including with more hours of observation.

Introduction

Modern zoos aim to enhance natural behaviour whilst ensuring optimal health conditions for their animals. Feeding presents an obvious opportunity for this, as natural feed items may stimulate natural feeding behaviour without compromising nutritional requirements. In carnivores like jaguars *Panthera onca*, feeding behaviour such as hunting, killing, dissecting, consuming and guarding prey would take up a certain amount of the time budget in the wild (Lindburg 1988). Although feeding live prey would indeed stimulate natural hunting, killing and dissecting behaviour of jaguars in captivity, the evident suffering on the part of the prey animal precludes this option on ethical grounds, and is therefore prohibited by animal protection laws in many countries. Hence, the challenge of carnivore feeding is to stimulate natural feeding behaviour without using live prey animals.

In zoos, jaguars may be fed processed meat, lean meat, parts of a carcass or whole prey (whole dead animals including viscera, skin and bones at varying amounts) (AZA Jaguar SSP 2016). Studies on different carnivores have shown that feeding with whole prey, carcasses, bones or frozen fish have led to an increase in consumptive and foraging behaviour, compared to when zoo felids were fed processed meat (Bashaw et al. 2003; Bond and Lindburg 1990; Iske et al. 2018; McPhee 2002; Skibiel et al. 2007; Stark 2005). Furthermore, some of these feeding methods have led to a decrease in or total eradication of stereotypic pacing behaviour (Bashaw et al. 2003; McPhee 2002; Skibiel et al. 2007; Stark 2005).

The objective of this study was to investigate how two different feed types (lean beef and whole rabbits) affect the behaviour of zoo jaguars for the first six hours after feed presentation. The ways in which the two feed types affected feeding behaviour, affiliative and agonistic social behaviour, stereotypic pacing behaviour and non-social active behaviour as well as non-social inactivity were investigated. The hypotheses were as follows: i) consumption time is affected by feed type in that more complex feed (whole prey) takes longer for the jaguars to consume than lean meat; ii) a higher proportion of social behaviour is affiliative rather than agonistic when whole prey is fed compared to lean meat as the jaguars are more satiated by the whole prey than by the lean meat; iii) the non-social active and inactive behaviours are affected by the feed type in that more complex feed (whole prey) increases the level of non-social inactive behaviour (resting) post feeding; and iv) the amount of stereotypic pacing behaviour post feeding is affected by feed type in that other studies have shown that more complex feeding (whole prey) may decrease abnormal behaviour (McPhee 2002; Skibiel et al. 2007; Stark 2005).

Materials and methods

Animals and husbandry

The study was carried out between January and March 2020 at Parken Zoo, Eskilstuna in Sweden. The group was comprised of three socially housed jaguars: two female siblings (aged 10 years and weighing 62.4 and 63.4 kg) and one male (aged 11 years, 81 kg). The animals were born and raised in captivity. They had access to an indoor (35 m^2) as well as a large outdoor (approximately 500 m^2) enclosure at different times of the day. Normally, the jaguars also had access to an additional indoor enclosure (32 m^2), but this was closed off during the study due to limited camera coverage. The indoor enclosure had a concrete floor and contained three large shelves (2–3 m^2) fixed at different heights of 1.5–2 m, a box (2 m^2) with straw and sawdust bedding and several logs of wood.

The jaguars were normally fed three times per week in the indoor enclosure. Each jaguar was fed 2–2.5 kg of carcass (shanks of cow/horse, including skin and bones). At approximately 1500, the jaguars were let in from the outdoor enclosure to find the feed, placed at three different locations to facilitate individual feeding. At irregular intervals, the jaguars were also fed whole, unopened sheep carcasses or rabbits. For the study, the jaguars were fed with each feed type for 10 consecutive feeding days. The feedings followed the normal feeding schedule and the jaguars were fed three times a week (Tuesday, Thursday and Sunday). The feedings were held at the same time of day (1520–1530) where possible to avoid influence of time of day. During the study, the enrichment routine was kept as normal, where small amounts of edible enrichments (chicken skin and feet, blood) were hidden every morning in the outdoor enclosure.

One feeding treatment consisted of lean beef feeding with only meat—no ligaments, skin/fur, bones or viscera. The beef was provided by Djurtjänst I Bollnäs AB in Sweden and was cut into the desired amount as one piece of meat without skin and fat lumps. The piece of meat was too large to be swallowed whole; animals had to chew off individual pieces. Before feeding the meat was covered with a mineral supplement (Effekt Sp Kolmården, Lantmännen Lantbruk Maskin, Sweden) at a dose of 30 g for the male and 25 g for each female. The second feeding treatment consisted of whole prey feeding. Whole defrosted rabbits were used, including meat, bones, fur/skin, other ligaments, viscera and heads. The jaguars had been fed rabbits before and were hence familiar with this kind of feed. The rabbits were provided from a local farmer. Each rabbit was weighed; parts of the legs were cut off if necessary to reach the desired amount. The jaguars were fed with the same amounts of feed for both treatments to make the consumption time comparable. At each feeding, the male received 2.5 kg and the females 2 kg of feed, based on the keepers' experience of the amounts the jaguars were fed on a normal basis.

Study design and behavioural observations

Data were recorded with Axis P3375-LV cameras (Axis Communications, Lund, Sweden) installed in the indoor enclosure. The camera was located approximately 3 m above the floor in the corners, overlooking the enclosure. The video recordings were automatically saved on a local server. Data were recorded over a time period of almost 4 weeks, consisting of ten feeding days for each feed type. Video recordings were saved from the time point when the jaguars were presented with the feed until six hours afterwards (1500 to 2200). Each individual jaguar was observed with continuous focal sampling for the first two hours after feed presentation, using Animal Behavior Pro, Version 1.5 (Newton-Fisher 2020). They were also observed for the whole six hours after feed presentation using instantaneous scan sampling at five-minute intervals, with data manually recorded (Martin and Bateson 1993). There was a total of 60 observations for the whole rabbit treatment and 42 observations for the lean beef treatment, because of server failure on the first three days of the latter treatment.

The ethogram (Table 1) was based on a standardised ethogram for Felidae (Stanton et al. 2015), with inspiration from a similar study on the effect of carcass feeding on captive tiger behaviour two hours after feeding (Stark 2005) and video recordings of the jaguars before the experiment at Parken Zoo.

Data were analysed in R using packages "car" (Fox and Weisberg 2019), "lmerTest" (Kuznetsova et al. 2017) and "MuMIn" (Bartoń 2013). The effect of feed type on the time spent in each behaviour (seconds) was evaluated using mixed effects linear models in which both the individual animal and the day of observation were included as random factors, and the feeding method as a fixed factor. In the case of non-normally distributed residuals, models were repeated with log-transformed data and if residuals of those were still not normally distributed, models were repeated with ranked data. The number of scans during which a behaviour was observed during the six hours after feeding were compared between feed types, using mixed effects linear models in which both the individual animal and the day of observation were included as random factors, and the feeding method and the hour of observation (1–6 hours after feeding) as fixed factors. Analyses were performed with ranked data. Because agonistic behaviour was not observed in the observation scans, it was not included in the analyses. The significance level was set to 0.05; P values between 0.05 and 0.10 were considered as trends.

Results

When the jaguars were fed raw muscle meat they started by licking off the mineral powder, and then chewed and ripped off smaller pieces of meat using their teeth and tongue. When fed whole rabbits, all jaguars consumed the rabbit starting from the head and moving down towards the hindquarters.

The jaguars spent significantly longer feeding when fed on whole rabbits compared with lean beef of the same weight, but without differences between days (Table 2). Furthermore, the jaguars showed more affiliative as well as agonistic behaviour during the two hours after they were fed lean beef compared to when they were fed whole rabbits. There was no significant difference between the time spent on non-social active, non-social inactive or stereotypic behaviour for the two feed types (Table 2). The three jaguars varied significantly in feeding time and levels of agonistic behaviour, stereotypic behaviour and non-social active behaviours shown. The time spent on non-social activity, and agonistic and affiliative behaviours varied between days.

When analysing the frequency of different behaviours during six hours after feeding, results confirm that feeding behaviour occurred significantly more when fed whole rabbits, particularly during the first hour after feed presentation. Irrespective of the feed type, feeding behaviour only occurred during the first hour (Table 3, Figure 1). There was no difference in the frequency of non-social active behaviour over the 6 hours post feeding

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Table 1. Ethogram used for jaguars *Panthera onca* in the present study

Category	Behavior	Description
Feeding	Consumption behavior	Jaguar consuming, eating, chewing, or manipulating feed, including licking, sniffing, and carrying the feed.
Non-social active behavior	Exploration/ locomotion	Jaguar moves around – including attentively while sniffing the ground and/or objects.
	Jump/climb	Jaguar leaps from one point to another (vertically or horizontally).
	Standing	Jaguar is in an upright position and immobile, with all four paws on the ground and legs extended, supporting the body.
	Groom	Jaguar cleans itself by licking, scratching, biting, or chewing the fur on its body, also include, licking paw and wiping it over its head. Grooming can occur when the individual is either standing, sitting, or lying down alone or during huddling.
Non-social inactive	Lying down/ sleeping	Jaguar's body is on the ground in a horizontal position, including on its side, back, belly or curled in a circular formation. The jaguar is not engaged in any other when lying down. Includes lying on the ground with head down and eyes closed.
	Sitting	Jaguar is in an upright position, with the hind legs flexed and resting on the ground, while front legs are extended and straight. The Jaguar is not engaged in any other than sitting.
Stereotypic	Pacing	Repetitive locomotion in a fixed pattern, such as back and forth along the same route. Can include walking, trotting, and running. Movement seems to have no apparent goal or function and can include small variations, such as the animal stopping for 2-3 seconds to explore. Must be performed at least two times in succession before qualifying as stereotypic.
Agonistic	Threaten	Jaguar directs aggressive s towards another jaguar (includes baring teeth, folding back the ears, slapping the ground, growling, raising the paw, snarling, and striking).
	Fight	Jaguar engages in physical combat with another jaguar. Some indicators for fight: ears are pinned back to the head, teeth are bared, sudden short fast movements, strikes with paw directed to the upper body and head area, a lot of vocalization.
Affiliative	Play	Jaguar interacts with another jaguar in "non-serious" manner (i.e. where there is no intention to threaten or harm). Some indicators for play are: ears raised/relaxed or slightly laid back, often full body contact similar to wrestling, soft bites, open mouth but no bearing of teeth, slight vocalization.
		Jaguar licks the fur of another jaguar's head or body.
	Nuzzle	Jaguar moves its entire head and nose side to side against one area of the head and body of another jaguar.
	Huddling	Jaguar is lying or sitting with body in contact with another jaguar. If the other jaguar is huddling with another individual, that individual is included in the huddling.
	Other incl. out-of-sight	Other including when an individual is not visible in the video.

between the two feed types (Table 3). The jaguars were most active during the first hour post feeding. Activity decreased in the following hours but increased again at four hours after feeding. Affiliative behaviour was the only behaviour observed to increase in frequency over time after feeding; the frequency of affiliative behaviour changed between days rather than with feed type.

Table 2. Results of statistical testing for an effect of feed type on the duration of various behaviors in the first two hours after feed presentation in linear mixed effects models that included individual and day as random factors; significant differences using [a], trend using [b]. # log-transformed data, ° ranked data, brackets (random factor individual, random factor day: * significant, - not significant).

Dependent	Mean ± SD duration (min)		F	P
	whole prey	lean meat		
Feeding# (*,-)	17±4	5±3	175.068[a]	<0.001[a]
Affiliative (-,*)	24±22	44±32	11.181[a]	<0.001[a]
Agonistic° (*,*)	0.02±0.06	0.05±0.05	6.190[a]	0.013[a]
Stereotyping° (*,-)	11±17	11±13	0.180	0.671
Other (*,*)	11±9	12±12	0.009	0.923
Non-social activity (*,*)	32±12	29±10	3.229[b]	0.072[b]
Non-social inactivity (-,-)	26±17	19±18	1.887	0.170

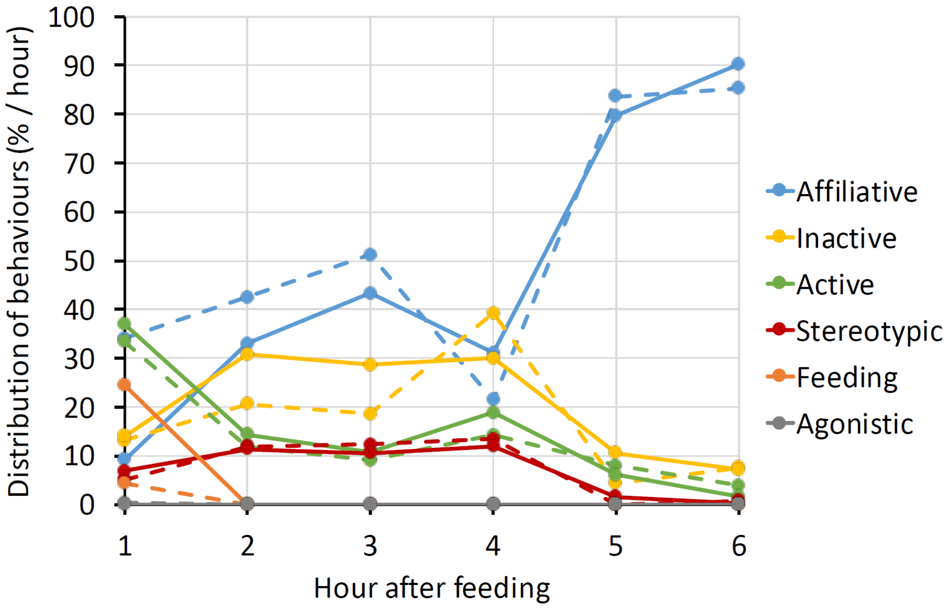

Figure 1. Distribution of different behaviours during six hours post feeding for jaguars *Panthera onca* fed whole prey (solid lines) or lean meat (broken lines).

Towards the end of the observation hours the animals were observed huddling more, resulting in the increase in affiliative behaviour in the hours after feeding. The frequency of stereotypic behaviour was not significantly affected by feed type (Table 3) but was also most distinct in the first few hours after feeding.

Discussion

An increased time spent on feeding when exotic felids are provided with a feed of a more complex structure compared to processed meat has been reported repeatedly (Bond and Lindburg 1990; McPhee 2002; Skibiel et al. 2007; Stark 2005). McPhee (2002) reported an increase in feeding time from <6 min to 62 min when African lions *Panthera leo*, African leopards *Panthera pardus pardus* and snow leopards *Panthera uncia* were fed calf carcasses compared to a traditional processed diet.

In the present study, replacing a piece of muscle meat with an equivalent amount of whole rabbit led to an increase in feeding duration from 5 to 17 minutes. Even though feeding time increased by more than 300%, in terms of the overall proportion of a 24-hour budget this represents a change of less than 1%. This leads to considerations about whether the increase in feeding time or the triggering of a specific mental disposition by the whole carcasses were the reasons for some differences in the other behaviours in this study.

McPhee (2002) found a larger increase in feeding time when lions and leopards were provided carcasses compared to processed diets. Furthermore, Stark (2005) found an increase in feeding time when three tigers were fed half a calf carcass compared to their regular daily enrichment consisting of large barrels, a spice bag or treat bag filled with processed meat or beef chunks. These authors used half or whole calf carcasses, much larger than the whole rabbits used in the present study, and did not ensure that the amount of food between the different feeding regimes was similar. Hence, their results will reflect not only differences in feed complexity but also in sheer bulk. The fact that ingestion of a processed meat diet occurred at a similar fast rate (during 5 min) as the ingestion of a chunk of meat in the present study suggests that pure muscle meat should not be considered more complex than minced meat, in terms of processing required by large felids. However, it might take longer before the muscle meat is disintegrated sufficiently in the stomach so that it can pass into the small intestine and this may have some effect on stomach fill-based satiety. Greater increases in feeding time and a larger effect on the other behaviours could potentially be achieved by providing larger carcasses and by making the feed harder for the jaguars to acquire.

Table 2 and Figure 1 show that feeding aroused the jaguars, and that depending on the effort required for feeding, the jaguars were either less inactive afterwards and showed more social

Table 3. The effects of feed type on the frequency of different behaviors (feeding, non-social activity, non-social inactivity, stereotypic, agonistic, and affiliative) during each of the six hours after feed was presented. Brackets (random factor individual, random factor day): * significant, - not significant.

Behaviour	Feed type	Time after feeding
Feeding (-,-)	<0.001 (higher on carcass)	<0.001 (decreasing)
Affiliative (-,*)	0.116	<0.001 (increasing)
Stereotyping (*,*)	0.983	<0.001 (decreasing)
Other (*,*)	0.247	<0.001 (decreasing)
Non-social activity (-,-)	0.667	<0.001 (decreasing)
Non-social inactivity (-,*)	0.452	0.004 (decreasing)

behaviour (when fed lean meat) or had higher levels of inactivity (when fed whole prey) afterwards. Note that in this particular group of jaguars, agonistic behaviours were extremely rare and therefore increased general activity led to a more distinct increase in affiliative rather than agonistic behaviour. This should not be interpreted as a social behaviour-stimulating effect of lean meat, but as a general state of arousal that in this particular group led to more positive interactions. In other individuals, this increased arousal might have led to increased agonistic or stereotypic behaviours in the respective time window, with the same effect of the feeding regime on the overall activity.

The interpretation of a general feeding-triggered state of arousal may be relevant for another aspect of interpreting stereotypies. In this study, which did not include the time before feeding, pacing was observed throughout the six hours after feeding, in parallel to other overall activity, with a decrease in hours five and six. Carlstead (1998) stated that feed-related pacing in carnivores takes place mainly pre-feeding as an anticipatory behaviour. This is further supported by de Jonge et al. (1986), Hönig and Gusset (2010) and Mallapur and Chellam (2002), who observed the same in felids and mink. However, referring to pacing observed after a feeding event as 'non-feed related' may be problematic if there is no separating period of a distinctively different behaviour between the feeding and the pacing. Carlstead (1998) stated that non-feed related pacing behaviour is mostly observed post feeding, yet the present study suggests that post-feeding pacing might be interpreted as a state of arousal triggered by the feeding event that was not 'used up', in terms of its activity-triggering potential, by that same feeding event. However, to test whether the pacing seen in this group of jaguars is triggered by the feeding event or has another origin, it would be necessary to observe the animals for longer periods of the day.

An evident limitation of the present study is the constraint in the time after feeding for which the animals could be assessed. In theory, whole prey feeding could lead to protracted digestion due to the larger proportion of indigestible or more difficult to digest material and therefore may result in longer lasting satiety. Further research on satiety linked to the digestion of animal fibre and its effect on behaviour would be informative. Whether whole prey feeding has this effect would need to be assessed by monitoring behaviour well through the second day after feeding.

The present study followed the feeding regime of the zoo, where 2–2.5 kg meat was offered three times per week. In their natural habitat, jaguars prey on a wide range of different species (Seymour 1989) with an average prey size of about 16 to 25 kg (De Cuyper et al. 2019; Núñez et al. 2000) and an estimated kill frequency of one kill every four to five days (De Cuyper et al. 2019). Jaguars can lay up to two and a half days guarding their kill and feeding repeatedly on it (Sunquist and Sunquist 2002). These natural feeding behaviours on larger carcasses include carcass guarding and feeding on a single carcass over more than one meal. It would be interesting to assess whether such a feeding regime would lead to a reduction in the behavioural arousal hypothetically linked to individual, small food portions. In zoos, a feeding regime of large carcasses might be applied for individually housed jaguars without any feeding competition over the remaining carcass pieces. In socially housed jaguars, the level of agonistic behaviour in response to a shared large carcass may vary with group size, composition and familiarity of the individual jaguars.

When hunting their natural prey such as capybaras, jaguars typically do not ingest the skull or the intestinal tract and may actually remove the gastrointestinal tract from the carcass (Schaller and Vasconcelos 1978), in contrast to the complete consumption of rabbits in the present study. This may be another indication that small carcasses such as a whole rabbit will not facilitate the feeding behaviours typical of free-ranging large felids, and consequently also will not yield comparable prey processing times. Notably, at Parken Zoo, this same group of jaguars is regularly provided with whole, freshly killed sheep carcasses, for which processing usually takes much longer than 20 minutes (A. Burkevica, personal observation). Further detailed documentation of the feeding of such large carcasses is recommended.

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