JZAR JOURNAL OF ZOO AND AQUARIUM RESEARCH
www.jzar.org

JZAR Research article

OPEN ACCESS

Research article

Feasts and fasts: the impact of feeding regimes on the activity budgets of zoo-housed jaguars *Panthera onca*

Rianna Brunner[1], Anita Burkevica[2], Jenny Gustafsson[2], Julia Johnsson[2], Peter Lundgren[2], Paul Wilhelm Dierkes[3] and Marcus Clauss[1]

[1]Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Zurich, Switzerland;
[2]Parken Zoo, Flackstavägen 13, 63222 Eskilstuna, Sweden
[3]Department of Bioscience Education and Zoo Biology, Goethe University Frankfurt, Frankfurt, Germany

Correspondence: Marcus Clauss, email; mclauss@vetclinics.uzh.ch

Keywords: activity budget, feeding, jaguar, stereotypies, whole carcass

Article history:
Received: 17 Mar 25
Accepted: 19 Jan 26

Abstract

Feeding practices are critical for the welfare of zoo-housed carnivores, yet zoo diets often lack the complexity of natural prey, potentially reducing stimulation and increasing stereotypic behaviours. This study examined how different food items combined with a fasting regime influenced the behaviour and activity budgets of three jaguars *Panthera onca* over eight weeks. Four feeding treatments were tested: featherless chicken, feathered chicken, beef meat without skin on bone (all with three feeding, four fasting days per week), and whole sheep or goat carcasses (two feeding, five fasting days per week). Behaviours were recorded continuously based on an ethogram, and beta regression mixed-effects models were used for analysis. Whole carcasses elicited the longest feeding times (88±21 minutes), compared to meat on bone (58±23 minutes) and chicken (32±10 minutes feathered, 12±4 minutes featherless) on feeding days. Large carcasses also encouraged unique behaviours such as food carrying, guarding, and manipulation, while providing intermittent feeding opportunities and possibly prolonged satiation. Although these differences were evident in feeding-related behaviours, overall activity budgets remained largely stable, and stereotypic pacing was not substantially affected by diet composition or fasting schedules. These findings underscore the enrichment potential of whole carcasses in promoting natural behaviours and enhancing feeding engagement. Zoos may benefit from incorporating more varied and naturalistic feeding regimes to improve animal welfare.

Introduction

Husbandry practices in zoos are critical for the physical and psychological health of their animals. Zoos strive to continuously improve animal welfare by expanding their knowledge of each species and incorporating this understanding into detailed guidelines (e.g. Podturkin and Papaeva 2020; EAZA Jaguar Best Practice Guidelines 2022). These guidelines are essential for creating environments that meet the biological and behavioural needs of the animals, allowing them to live long (Roller et al. 2021) and meaningful (Clauss and Schiffmann 2023) lives. To ensure their purpose, husbandry practices should not remain static but evolve through ongoing re-evaluation.

Ex-situ environments differ significantly from the wild in terms of space, predator-prey interactions and resource availability, amongst others. Large terrestrial carnivores, typically apex predators with extensive home ranges, are especially prone to developing stereotypic behaviours, i.e. repetitive behavioural patterns that lack an apparent goal and often indicate stress or frustration (Mason 1991). Stereotypic behaviours, such as pacing, tail-sucking, or repetitive grooming, are commonly observed in carnivores and are considered indicators of reduced welfare (Clubb and Mason 2003; Morris 2018). In zoos, these behaviours have been linked to several factors, including restricted space compared to natural home range size (Clubb and Mason 2003; Kroshko et al. 2016), the density and noise intensity of zoo visitors (Mallapur and Chellam 2002; Sellinger and Ha 2005; Suárez et al. 2017), and feeding practices (Lyons et al. 1997; Bashaw et al. 2003). Additionally, pacing, the most common stereotypy observed in carnivores (Mason et

https://doi.org/ 10.19227/jzar.v14i1.937

al. 2007), is also a typical behaviour associated with anticipation (Anderson et al. 2020; Krebs et al. 2022).

Feeding dynamics of wild carnivores are complex, involving irregular meal patterns and energy-intensive hunting processes (De Cuyper et al. 2019). Larger carnivores, such as jaguars *Panthera onca*, often gorge-feed, consuming energy far beyond daily caloric requirements in a short period of time (Emerson et al. 2025). By contrast, zoo feeding schedules often provide processed meals at regular intervals, with limited fasting and naturalistic feeding opportunities. Studies have shown that while some zoos do incorporate fasting days, they are often brief, inconsistently applied and rarely preceded by gorge-feeding (Kleinlugtenbelt et al. 2023). Alternative feeding strategies, such as carcass feeding (McPhee 2002), scatter feeding (Andrews and Ha 2014), and other forms of enriched feeding (Jenny and Schmid 2002), have been explored but are not widespread as of today.

The present study set out to investigate whether the type of food item coupled with an adjusted fasting period affects the behaviour of zoo-housed jaguars. By comparing different degrees of food processing and examining the effects of fasting days, we aimed to determine whether less processed, more naturalistic food, coupled with a fasting schedule, promotes greater behavioural diversity and reduces the occurrence of stereotypic behaviours.

Material and Methods

Study species and husbandry

In this study, three jaguars housed at Parken Zoo, Eskilstuna, Sweden, were observed. The three individuals have been kept together in an enclosure since 2012. The group comprised two female siblings (Mocoa and Yupala), born in 2010, and one melanistic male (Avatar), born in 2009. These animals were previously studied in 2020 regarding the effects of feeding lean meat versus whole rabbit *Oryctolagus cuniculus* carcasses (Enemark et al. 2023). For the present study, data was collected from October to December 2023 and April 2024. Mocoa was most likely in heat in the first weeks of November.

The jaguar enclosure included two connected outdoor areas (500m² total) and one indoor area (35m², 4 metres high). The outdoor enclosure included two resting areas with straw bedding, a climbing wall, logs positioned both upright and horizontally, a pond, and natural vegetation, including trees. The indoor enclosure had a concrete floor, several shelves, and logs on the floor. One shelf and parts of the ground were covered with wood shavings and straw. Two drinking bowls were available outside and one inside. The jaguars were restricted to the outdoor area during the day (approximately 0900-1700 hrs) and only given access to the indoor enclosure at night. They were temporarily confined to the indoor facility for daily enclosure cleaning. Feeding took place exclusively outside between 0800 hrs and 1100 hrs, following the cleaning of the outdoor enclosures.

During this study, only olfactory enrichment was provided, such as laying blood traces and sprinkling spices. Food enrichment was given in very small amounts only when keepers were unable to move the jaguars to a desired enclosure. The pre-study routine was maintained as consistently as possible to minimise any behavioural effects due to changes in their daily schedule.

Feeding treatments

The jaguars were offered four different types of food items. The first food category, called “meat on bone,” consisted of beef pieces attached to bones but lacking fur, fat, connective tissue, or ligaments. On average, 12kg of this meat was provided to the group, divided into three pieces to reduce the risk of food aggression. Each piece was coated with around 30g of carnivore supplement powder (Effekt Sp Kolmården, Lantmännen Lantbruk Maskin, Sweden) and placed randomly in the enclosure.

The second and third food items were whole chickens (Ross 308), sourced from a local farmer and slaughtered by the zoo veterinarian (bolt gun stunning and neck dislocation) before being frozen whole. The chickens were seven weeks old at slaughter, including both sexes. For one treatment, the jaguars were fed whole chickens with feathers (average weight 2.2kg), while for the other treatment, the feathers and skin were removed (average weight 1.9kg). The young age of the chickens resulted in an underdeveloped plumage. During feeding, six chickens were scattered throughout the enclosure, two per individual as recommended by the keepers. However, the male often consumed three chickens, leaving one of the females with only one chicken.

The fourth food category consisted of fresh sheep (Gute breed, average 44.5 kg) or African dwarf goat carcasses (average 25.5 kg). Due to their large weight (average 35kg), whole carcasses were only offered twice weekly. The decision between species depended on availability, with the chosen animal slaughtered in the stable by the attending veterinarian using bolt gun stunning and exsanguination. Carcasses were hung by their hind legs on a wooden beam in the enclosure, approximately 2 metres off the ground, using a cord that gave way under sufficient pressure (which only the male seemed to be able to exert).

Each of the four food categories was applied for a seven-day period, with one repetition for each category, resulting in eight weeks of observation. Feeding occurred three times weekly (Tuesday, Thursday, Sunday) for all categories except large carcasses, which were provided twice weekly (Tuesday, Friday). The other days were fasting days.

A feeding day was defined as any 24-hour period during which food was provided, while a fasting day was when no new meat was offered. However, foraging did occur on fasting days when the jaguars were fed large food items (e.g. whole carcasses). Keepers recorded the type of enrichment given, the type of day and food weights before and after feeding. Additionally, daily environmental variables (minimum and maximum temperature, wind speed, and precipitation) were sourced from Vadret1.com (2024).

Study design and ethogram

To observe behaviour, jaguars were recorded using cameras: one camera in the inside enclosure (AXIS P3375-LV, Axis Communications AB, Lund, Sweden) and two in the outdoor areas (AXIS P1468-LE, Axis Communications AB, Lund, Sweden). Four additional cameras (VisorTech DSC-750.app V2, Pearl GmbH, Buggingen, Germany) were placed around the enclosure to minimise blind spots during October to December. Damaged server files necessitated repeating one week of feathered chicken feeding and one week of whole carcass feeding in April 2024, during which only the three main cameras were available.

Behaviour was analysed through focal sampling and continuous recording. A total of 1320 hours of footage were observed per individual using BORIS (v. 8.21.8, 2023-10-05) (Friard and Gamba 2016). Individuals were identified by coat colour and pattern.

The ethogram was adapted from a standardised ethogram for Felidae (Stanton et al. 2015) and one previously used for jaguars (Barbosa Santos et al. 2020), with additional behaviours identified during pre-study observations. In total, 32 behaviours were grouped into nine categories (Table 1). Stereotypies were divided into anticipatory pacing and stereotypic pacing. For analysis, the “Foraging” category included food acquisition, carrying, consumption, and manipulation.

Data analysis

A total of 3960 hours of video footage was coded and analysed using RStudio (Version 4.4.0), using the packages DHARMa (Hartig 2025), emmeans (Lenth and Piaskowski 2025), ggpubr (Kassambra

Table 1. Ethogram for jaguars *Panthera onca* used in the present study (adapted from Barbosa Santos et al. 2020; Stanton et al. 2015)

Behavioural category	Behavioural act	Description
Exploratory	Alert	Interruption of an activity and concentration of attention on something in the environment. Directing of the eyes towards a visual and/or auditory stimulus.
	Dig	Turning the ground or digging a hole with its paws.
	Manipulation	Uses any part of body to touch, hold, move, or pick up, an object.
	Play	Interaction with environment in a “non-serious” manner (i.e. where there is no intention to harm).
	Sniff	Inhaling environmental odours. The individual can direct themselves to the source of the odour or just sniff the air.
Foraging	Drink	Ingesting water by lapping it up with the tongue.
	Food acquisition	Animal works to acquire food (e.g. if placed at a difficult to reach location).
	Food carrying	Food is picked up off the ground and moved to another location.
	Food consumption	Ingestion of food by means of chewing with the teeth and swallowing.
	Food manipulation	Uses any part of body to touch, hold, move, or pick up, a food item (e.g. removal of feathers from food item) without ingesting it.
	Grazing	Selective biting or nibbling on grass or other vegetation.
Locomotion	Climbing	Ascends and/or descends an object or structure.
	Running	Forward locomotion in a rapid gait.
	Standing	Individual is in an upright position and immobile, with all four paws on the ground and legs extended, supporting the body.
	Walking	Forward locomotion at a slow gait.
Maintenance	Defecate	Release of faeces on the ground while in a squatting position.
	Groom	Cleaning by licking, scratching, biting or chewing the fur or other parts of the individual’s body. May also include the licking of a front paw and wiping it over one’s head.
	Urinate	Release of urine on the ground while in a squatting position.
Other	Out of sight	Individual is in a part of the enclosure where it is partly or completely out of view and recording behaviours is not feasible.
Reproductive	Attempted copulation	Male attempts to mount female but female rejects male by moving away or showing aggression towards male. Further if female does not reject male and male is attempting to mount female but does not display a positioning that makes successful copulation likely.
	Copulation	Male mounts female and intromission is achieved.
	Roll	While lying on the ground, the individual rotates body from one side to another. During the roll, the back is rubbed against ground, the belly is exposed, and all paws are in the air. Individual may continue rolling repeatedly from side to side.
Rest	Rest	Lying or sitting on the ground with eyes open and easily alerted to stimuli in the environment.
	Sleep	Lying down with the head down and eyes closed, performing minimal head or leg movement, and individual is not easily disturbed.
Social interaction	Aggression	Engagement in physical combat with conspecific or display of signs of aggression (i.e. hissing, ears back, showing teeth).
	Allogrooming	Individual licking the fur of conspecific.
	Human	Directed gaze or interaction with a human (e.g. zookeepers, visitors).
	Social face rub	Rubbing the side of one’s face on another individual.
	Social play	Interaction with conspecific in a “non-serious” manner (i.e. where agonistic behaviours are absent (i.e. hissing, ears back)
Stereotypies	Anticipatory pacing	Repetitive locomotion in response to a stimulus or in anticipation of an event, often combined with regular gazing in that direction. Must be performed at least two times in succession before qualifying as 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. Must be performed at least two times in succession before qualifying as stereotypic.

2025), glmmTMB (Brooks et al. 2017), lme4 (Bates et al. 2015) and MuMln (Bartoń 2025). Due to the large number of observed behaviours, the analysis focused on specific behaviours and categories, particularly “Foraging” and “Locomotion.” Categories such as “Rest” and “Stereotypes” were broken down into individual behaviours, including Rest, Sleep, Anticipatory Pacing, and Stereotypic Pacing.

Although third fasting days during whole carcass weeks were included in the analysis, they were only used to indicate trends, as they were based on few observation data (two days per individual).

Beta regression mixed-effects models with the option for zero inflation were used to assess the effects of food type and fasting days on jaguar behaviours. Fixed effects included diet and fasting day, while random effects accounted for individual and environmental factors. The models included the additive effects of the food category and fasting day as fixed effects, making it possible to estimate the independent contribution of each factor to behavioural changes. Additionally, models with an interaction term were fitted, to test whether fasting effects depended on food type. Estimated Marginal Means (EMMs) were calculated to represent adjusted behavioural averages and were used for pairwise comparisons (z-tests) across feeding conditions and fasting days; however, raw data are presented throughout. For foraging behaviours, convergence issues in interaction models, due to numerous zeros on fasting days, necessitated the use of ranked linear mixed-effects models. EMMs were compared using t-tests.

Additional results for behavioural categories not included in the main results section, as well as analyses of differences between subjects, weeks, days, the influence of environmental variables, and activity budgets in the first hours after feeding can be obtained from the corresponding author.

This study complied with the EAZA Code of Ethics and the guidelines for the care and management of zoo and wild animal species in captivity. As behavioural data were collected using video cameras, no additional ethical approval was required. This non-invasive recording method minimised disturbance to the jaguars and posed no risk of harm. The zoo provided consent for their animals to participate in this study.

Results

Throughout the study, resting was the most predominant behaviour, accounting for 73.7±8.8% (17.7±2.1 h/d) of a 24-hour cycle. Within this category, sleeping occupied more time than general resting, comprising 45.3±9.8% (10.9±2.3 h/d), while resting accounted for 28.4±8.9% (6.8±2.1 h/d). Locomotion was the second most common behaviour, making up 14.8±7.4% (3.6±1.8 h/d) of the daily cycle. On average, all other behavioural categories contributed less than 5% to the daily activity budget. Anticipatory pacing and stereotypic pacing contributed on average 0.4±0.5% (5.9±7.8 min/d) and 1.1±1.8% (15.3±25.8 min/d), respectively. Foraging constituted 1.7±2.3% (24.4±33.5 min/d) of the daily activity budget when averaged across all days and subjects. Furthermore, an overview of the amount of daily time spent on each behaviour by food item and type of day is available in Table 2.

Foraging

When averaged across all weekdays (including fasting days), significant differences were observed in the time jaguars spent foraging between food items. They foraged for an average of 5±6 min/d for featherless chicken, 14±17 min/d for feathered chicken, 27±33 min/d for meat on bone, and 51±44 min/d for whole carcasses. Foraging times were significantly higher on feeding days (44±31 min) compared to fasting days (12±28 min), with the first two fasting days showing comparable levels (Figure 1a).

Considering only feeding days specifically, foraging times were: featherless chicken 12±4 min/d, feathered chicken 32±10 min/d, meat on bone 58±23 min/d, and whole carcass 88±21 min/d (Figure 1a). Foraging times for feathered and featherless chicken were not significantly different, nor were they for meat on bone and whole carcass. However, both meat on bone and whole carcass required significantly more time for consumption than featherless chicken. On the day after feeding, foraging dropped to zero for all food types except whole carcass, which retained a similar duration to the previous day (72±40 min/d), indicating prolonged feeding. By the second fasting day (17±26 min), foraging time for whole carcass was no longer significantly different from the other categories.

Food carrying was similar across food items on feeding days (average 1±1 min/d) but increased the following day for whole carcass (2±2 min/d). Food acquisition was only observed during whole carcass feeding (5±3 min/d) due to the carcass being hung up. Food manipulation, such as removing feathers or fur, occurred at comparable levels for feathered chicken (2±2 min/d) and whole carcass (4±3 min/d) on the feeding day and was nearly absent in other categories.

Locomotion

When averaged across all weekdays (including fasting days), locomotion was less prevalent during whole carcass feeding (175±109 min/d) compared to featherless chicken (236±81 min/d, +35%) and meat on bone (259±101 min/d, +48%), but not significantly different from feathered chicken (187±112 min/d). The time spent moving also differed when comparing jaguars being fed feathered chicken (187±112 min/d) versus meat on bone (259±101 min/d, +39%). Locomotion was lower on feeding days (184±73 min/d, -21%) than on fasting days (233±120 min/d, Figure 1b).

Locomotion showed a trend of increasing with time since the last meal, peaking on the second fasting day (average 263±42 min/d, Figure 1b) for all categories except whole carcass. On feeding days, locomotion was lowest for feathered chicken (123±51 min/d), significantly less than featherless chicken (210±55 min/d) and meat on bone (224±83 min/d), but comparable to whole carcass (176±48 min/d).

For whole carcass, locomotion dropped significantly on the first fasting day (115±92 min/d, -35%) before returning to feeding day levels (176±48 min/d) on subsequent days and was on average lower than on all other food items on that day. On the second fasting day of whole carcass weeks, locomotion was reduced compared to meat on bone but not the chicken phases.

Locomotion differed significantly among individuals (χ^2=68.98, P<0.001), with the male showing the highest levels (271 min/d) compared to the females (142 and 219 min/d). The male exhibited minimal climbing behaviour (median 0 min/d) compared to the females (1 and 3 min/d).

Resting

When averaged across all weekdays (including fasting days), sleeping time varied between chicken treatments, with featherless chicken resulting in less sleep (680±91 min/d, -5%) than feathered chicken (715±155 min/d). Meat on bone had the lowest sleep duration (567±88 min/d, -26% compared to feathered chicken), while whole carcass was intermediate (641±166 min/d, Figure 1c). When resting time was considered, the only significant difference was between feathered chicken (395±149 min/d) and meat on bone (415±105 min/d, Figure 1d). Resting time remained consistent across days (Figure 1d), but sleeping time dropped significantly on the second fasting day compared to feeding days (596±159 vs. 687±153 min/d, Figure 1c).

Considering only feeding days specifically, sleeping time was highest for feathered chicken (794±191 min/d) and lowest for meat on bone (572±85 min/d), with featherless chicken and whole carcass at intermediate levels (723±64 and 648±141 min/d, respectively, Figure 1). During fasting, sleeping time was consistently lower in meat on bone weeks compared to feathered chicken and whole carcass but not significantly different from featherless chicken. Within categories, sleep duration was stable across day types, except for feathered chicken, where it declined from feeding days (797±76 min/d) to fasting days (667±76 and

Table 2. Daily activity budget (in minutes per day, means±SD of the raw data) of the three jaguars *Pantheroa onca* of the present study depending on diet and feeding or fasting day.

Behaviour (mind/day)	Chicken without			Chicken with			Meat on bone			Whole carcass			
Fasting day	0	1	2	0	1	2	0	1	2	0	1	2	3
Exploratory	17± 11	12± 7	15± 15	9± 3	10± 5	9± 5	7± 6	8± 5	10± 4	12± 6	11± 8	10± 5	8± 4
Alert	8± 7	5± 4	9± 11	2± 2	3± 2	3± 2	3± 5	3± 5	4± 4	6± 4	4± 7	3± 3	4± 3
Dig	0± 0	0± 0	0± 0	0± 0	0± 0	0± 0	0± 0	0± 0	0± 0	0± 1	0± 0	0± 0	0± 0
Manipulation	1± 0	2± 2	1± 0	1± 0	1± 1	1± 1	0± 1	1± 1	1± 1	1± 0	0± 0	1± 1	1± 1
Play	0± 0	0± 0	0± 0	0± 0	0± 1	0± 0	0± 1	0± 0	0± 0	0± 0	0± 0	1± 1	0± 0
Sniff	8± 5	5± 3	5± 4	6± 3	5± 3	5± 3	3± 2	4± 4	5± 2	6± 4	6± 4	5± 3	4± 2
Foraging	12± 4	0± 0	0± 0	32± 10	0± 1	0± 0	58± 23	1± 0	0± 0	88± 21	72± 40	17± 26	8± 15
Food acquisition	0± 0	0± 0	0± 0	0± 0	0± 0	0± 0	0± 0	0± 0	0± 0	5± 3	0± 0	0± 0	0± 0
Food carrying	0± 0	0± 0	0± 0	1± 0	0± 0	0± 0	1± 2	0± 0	0± 0	3± 4	2± 2	1± 2	0± 0
Food consumption	12± 4	0± 0	0± 0	28± 10	0± 1	0± 0	57± 22	1± 3	0± 0	75± 18	70± 37	16± 25	7± 15
Food manipulation	0± 0	0± 0	0± 0	2± 2	0± 0	0± 0	0± 0	0± 0	0± 0	4± 3	1± 1	0± 1	0± 0
Grazing	0± 1	2± 4	8± 11	2± 5	3± 8	13± 28	0± 1	0± 0	0± 0	3± 7	0± 1	2± 7	1± 1
Drink	1± 1	0± 1	1± 1	1± 1	1± 1	1± 1	1± 1	0± 0	1± 1	2± 1	1± 1	1± 1	0± 0
Locomotion	210± 55	256± 100	258± 70	123± 51	226± 116	260± 145	224± 83	278± 106	317± 109	176± 48	115± 92	215± 144	214± 118
Climbing	2± 2	3± 2	3± 4	1± 1	3± 3	4± 5	4± 4	6± 5	8± 6	1± 1	1± 2	2± 2	4± 5
Running	1± 0	1± 0	1± 1	0± 0	0± 0	1± 0	1± 1	1± 0	1± 0	1± 0	0± 0	0± 0	0± 0
Standing	67± 46	74± 60	82± 56	41± 28	41± 22	44± 26	74± 77	93± 99	113± 89	69± 30	40± 23	42± 28	38± 18
Walking	142± 66	181± 89	175± 80	82± 44	184± 103	216± 130	149± 73	184± 98	204± 123	106± 39	75± 83	173± 134	176± 108
Maintenance	22± 7	29± 13	32± 15	17± 8	22± 13	21± 16	20± 7	16± 9	20± 5	21± 14	23± 11	27± 13	26± 17
Defecate	0± 0	1± 1	0± 0	0± 0	1± 0	0± 0	0± 0	0± 0	0± 0	0± 0	0± 0	1± 1	0± 0
Groom	21± 7	28± 13	31± 15	16± 8	21± 13	20± 16	19± 7	15± 8	19± 4	20± 14	22± 11	26± 13	25± 12
Urinate	1± 0	0± 0	0± 0	0± 0	0± 0	0± 0	0± 0	0± 0	0± 0	0± 0	0± 0	0± 0	0± 0
Reproduction	7± 8	10± 11	8± 7	2± 3	3± 4	1± 2	10± 12	20± 26	26± 29	2± 3	2± 6	2± 3	5± 5
Attempted copulation	2± 2	3± 2	3± 4	1± 1	3± 3	4± 5	4± 4	6± 5	8± 6	1± 1	1± 2	2± 2	4± 5
Copulation	3± 4	5± 7	4± 3	0± 1	1± 1	0± 0	3± 4	9± 14	9± 14	1± 1	1± 1	0± 0	1± 2
Roll	1± 1	1± 2	1± 1	0± 0	0± 0	0± 0	2± 4	4± 8	3± 7	0± 0	0± 0	1± 1	1± 1
Rest (category)	1089± 52	1039± 117	1012± 63	1189± 72	1061± 131	1017± 148	976± 129	1011± 111	927± 116	1063± 61	1161± 111	1062± 166	1069± 125
Rest	366± 64	379± 90	403± 109	395± 172	394± 136	396± 141	404± 122	411± 82	453± 110	415± 119	501± 114	423± 203	477± 169
Sleep	723± 64	660± 97	609± 92	794± 191	668± 72	620± 119	572± 85	599± 85	474± 16	648± 141	659± 128	639± 213	591± 206
Social Interaction	35± 15	40± 20	47± 27	25± 17	48± 31	50± 22	40± 23	32± 14	40± 17	18± 11	12± 10	33± 19	35± 26
Aggression	1± 1	1± 1	2± 2	1± 1	1± 1	2± 1	1± 1	1± 1	2± 2	1± 1	0± 0	1± 1	2± 2
Allogrooming	21± 12	19± 11	26± 9	14± 10	17± 8	17± 5	16± 14	15± 15	16± 21	9± 7	8± 6	17± 10	11± 6
Human	1± 0	1± 1	0± 1	1± 0	1± 1	0± 0	1± 1	1± 1	0± 0	1± 1	0± 1	1± 1	1± 0
Social face rub	0± 0	0± 1	0± 0	0± 1	0± 0	0± 0	0± 0	0± 0	0± 0	0± 0	0± 0	1± 1	0± 1
Social play	12± 12	19± 19	18± 20	9± 11	28± 26	30± 22	22± 23	15± 16	21± 18	7± 7	4± 6	14± 11	21± 21
Stereotypes	15± 12	24± 23	19± 16	12± 22	29± 44	26± 37	20± 21	24± 25	25± 30	14± 9	7± 14	31± 39	37± 39
Anticipatory pacing	8± 7	4± 4	9± 7	4± 4	1± 2	4± 5	9± 8	14± 14	7± 7	12± 10	1± 2	3± 5	1± 1
Pacing	7± 8	20± 21	10± 11	8± 21	27± 43	22± 36	14± 21	11± 15	18± 26	2± 4	6± 14	28± 38	36± 39

618±86 min/d, Figure 1).

Resting time was lower on the first fasting day in feathered chicken (394±136 min/d) compared to whole carcass (501±114 min/d, Figure 1). However, resting time within a category remained consistent regardless of day type.

While sleep duration was similar across individuals, resting

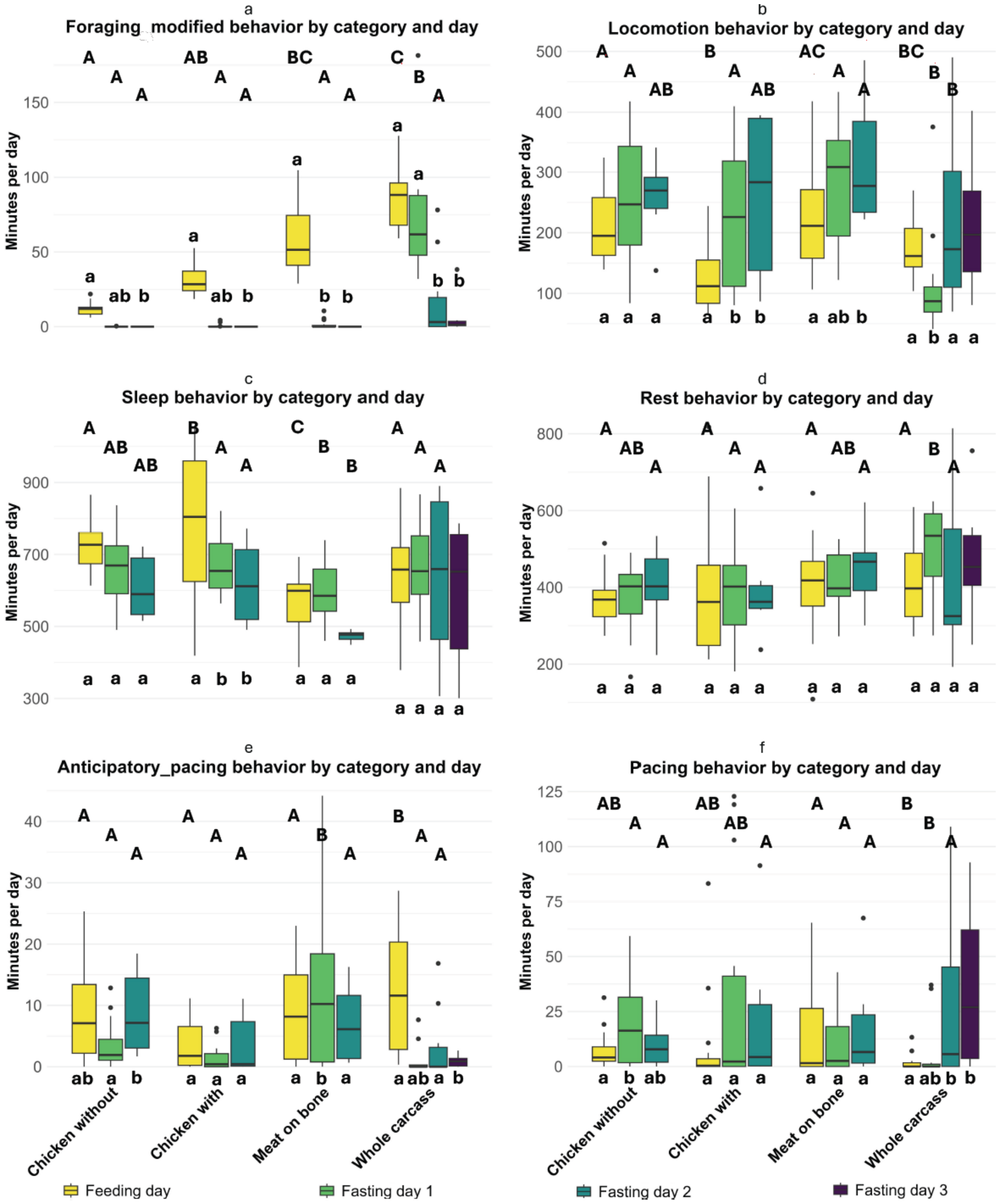

Figure 1. Boxplots of a) foraging, b) locomotion, c) sleeping, d) resting, e) anticipatory pacing and f) stereotypic pacing behaviour by type of day and food item. Different capital letters in the same row indicate significant differences between food items on a day; different small letters within a food item indicate significant differences between days for this food item.

behaviour varied significantly (χ²=49.85, P<0.001). One female rested the most (446 min/d), followed by the other female (389 min/d) and the male (321 min/d).

Stereotypies

When averaged across all weekdays (including fasting days), anticipatory pacing was more prevalent during whole carcass feeding weeks (5±8 min/d) compared to chicken feeding (featherless: 6±6 min/d; feathered: 3±4 min/d, Figure 1e) after adjusting for individual and seasonal effects. On whole carcass feeding days, cleaning of the enclosure and food distribution by keepers averaged 39±7 min/d, nearly double the time for other categories (featherless chicken: 25±10 min/d; feathered chicken: 18±2 min/d; meat on bone: 22±4 min/d). Stereotypic pacing was unaffected by food category or day type when modelled separately (Figures 1f). Overall, stereotypic behaviours remained stable on the feeding (15±17 min/d) and the first fasting day (22±30 min/d) but increased on the second fasting day compared to a feeding day (26±32 min). Stereotypic behaviours were most prevalent on the third fasting day (37±38 min/d) but not significantly different from other days due to strong individual variation, which was adjusted for in the model.

Anticipatory pacing was highest on feeding days with whole carcass (12±10 min/d) compared to other food types (average 7±3 min/d, Figure 1e). On the first fasting day, anticipatory pacing was highest during meat on bone (14±14 min/d) compared to the other categories (average 2±2 min/d). Whole carcass feeding showed reduced anticipatory pacing on fasting days compared to feeding days (12±5 min/d), but the effect was only significant on the third fasting day (1±1 min/d).

Stereotypic pacing remained relatively stable across all days and categories (Figure 1f). Whole carcass did show slightly reduced pacing on the feeding (2±4 min/d) and the first fasting day (6±14 min/d) compared to meat on bone days (14±21 min/d and 11±15 min/d). Within categories, pacing was largely consistent over time. Elevated pacing was observed for whole carcass on the third fasting day (36±39 min/d), but the limited data here necessitates cautious interpretation.

Stereotypic behaviours differed significantly among individuals (χ²=18.96, P<0.001). The male displayed the highest levels (23 min/d), followed by the females (14 and 3 min/d). The male also exhibited slightly more anticipatory pacing (7 min/d, P<0.05), while one female showed significantly less stereotypic pacing (median 0 min/d) compared to the other two animals (both median 9 min/d, 95% CI [0, 116] and [0, 63], respectively).

Discussion

This study examined how various food items paired with a fasting regime affected the behaviour and welfare of zoo-kept jaguars, focusing on behavioural diversity and the occurrence of stereotypic behaviours. Using 24-hour activity budgets allowed a comprehensive analysis of behaviour, capturing subtle responses often missed in shorter observations.

Several limitations should be considered when interpreting the findings of this study. The small sample size (three jaguars) limits the generalisability of results, and the reproductive cycle of one female significantly influenced group dynamics. During the two weeks of heightened reproductive activity, locomotion increased, while resting and sleeping time declined, with a slight rise in pacing during the first week. Additionally, seasonal variations, like increased grooming and social interactions during colder weather, highlight environmental influences on behaviour.

As expected, different food items led to variations in feeding times. The total weight of meat was not standardized between treatments, an impracticality given the differences in size between, for example, a whole sheep carcass and a chicken. Nonetheless, it was helpful to compare feeding durations to provide insight into how extended feeding bouts might affect the activity budgets. Wild jaguars are known to be opportunistic hunters (Garla et al. 2001), with prey sizes ranging from less than one kilogram to over 200 kilograms (Cavalcanti and Gese 2010). The food items chosen for this study partially reflected this natural variation.

Importantly, it is not just the numerical differences in foraging time that matter but how these differences translate into the overall activity budgets of the jaguars. While differences between individual food items may seem small, the cumulative effect over a month or more is relevant. When summed up, jaguars spent approximately one full day per month foraging when provided with whole carcasses, whereas for other food items, it was only a few hours at most. During the remaining time, the animals were largely inactive, as is to be expected for large predators (Jeschke 2007).

Studies on the activity budgets of wild jaguars are hard to come by. Most camera-trap (Harmsen et al. 2011; Dobbins et al. 2018; Jędrzejewski et al. 2021) and telemetry studies (Schaller and Crawshaw 1980; Cavalcanti and Gese 2009) focus on home ranges or activity patterns rather than activity budgets. Jaguar activity patterns vary significantly by site, likely reflecting adaptations to their primary prey's daily activity (Harmsen et al. 2011; Hernández-Saint Martín et al. 2013; Porfirio et al. 2017). For example, jaguars are predominantly nocturnal in some areas (Núñez et al. 2000; Harmsen et al. 2011), crepuscular in others (Maffei et al. 2004; Jędrzejewski et al. 2021), and even diurnal in the Brazilian Pantanal (Crawshaw and Quigley 1991).

In this study, jaguars spent about 18 hours daily resting or sleeping, mainly at night, with activity peaking during feeding times. Activity was highest between 0600 and 2000 hrs, likely influenced by the zoo's feeding schedule rather than natural cues. This contrasts with wild jaguars, whose activity is shaped by ecological factors like prey availability and moon phases (Harmsen et al. 2011). The zoo's location in Sweden caused significant seasonal daylight variations, from about six hours in late winter (25% of the day) to over 14 hours in spring (nearly 60%). Despite seasonal changes, activity patterns remained largely unaffected. This stability is likely due to the fixed daily schedule, which removes the need to align activity with hunting or territorial defence.

When comparing the two chicken treatments, we observed a notable, though not statistically significant, difference in feeding duration. Jaguars took an average of 20 minutes longer (+166%) to consume chickens with skin and feathers compared to featherless chickens, likely due to their apparent dislike of feathers, which required manipulation for their removal. However, despite this difference, it is crucial to note that in terms of overall activity budgets, these additional foraging times still accounted for only around 1% of a difference in the jaguar's daily activity. Similarly, Enemark et al. (2023) observed in their study that the jaguars took longer to feed and exhibited increased post-feeding arousal when provided with whole rabbit carcasses (17±4 min/d) compared to an equivalent weight of lean meat (5±3 min/d). Both studies demonstrated that more complex food items led to extended feeding times. However, these increases, while notable, only had a marginal effect on overall daily activity budgets. This highlights the importance of considering both short-term behavioural responses and long-term activity budgets when evaluating the welfare benefits of a species-appropriate diet.

We compared post-feeding arousal in our study with Enemark et al. (2023) by analysing jaguars' activity budgets during the six hours after feeding. In our study, pacing was virtually absent during this time, while Enemark et al. reported pacing at around 10% during the first four hours. Resting behaviours, such as lying down and sleeping, dominated shortly after feeding in our study but increased later in Enemark et al.'s research. These differences may be explained by feeding times: morning feeding (0900–1000 hrs) in our study versus late afternoon (1500 hrs) in Enemark et al.'s study. Overall, we observed fewer stereotypic behaviours and more resting, indicating no signs of excessive post-feeding arousal.

Whole carcasses prompted distinct behavioural dynamics, with foraging time on feeding days (6.11% of the feeding day) lasting about 30 minutes longer than with meat on bone (4.03% of the feeding day), though the difference was not significant. This aligns with previous research showing longer feeding bouts and processing times for whole carcasses (Bond and Lindburg 1990; McPhee et al. 2002; Stark 2005). Carcasses were typically consumed over two to three days, with the digestive tract often left the only part uneaten, a pattern also reported in wild jaguars (Schaller and Vasconcelos 1987). This extended availability of food influenced the daily activity patterns. Unlike smaller food items, which were usually consumed in one sitting, carcasses provided an opportunity for intermittent feeding. The jaguars alternated between feeding and resting, increasing nocturnal activity while showing little competition or aggression. The behaviour of returning to a kill over several days is also commonly observed in free-ranging jaguars feeding on large prey (Schaller and Vasconcelos 1987; Cavalcanti and Gese 2010; Jędrzejewski et al. 2014). Carcass feeding also promoted behaviours absent or rare with other food items, such as food-guarding toward keepers and carrying carcass portions to indoor areas or up enclosure structures. These behaviours highlight the enrichment potential of carcasses, encouraging problem-solving and physical exertion. While this effect of whole carcass feeding may be considered positive, it must be acknowledged that other aspects of the natural feeding behaviour of predators, such as searching for prey, hunting and killing (Veasey 2020), were not addressed by the food provision methods of the present study.

Fasting days increased locomotion, with jaguars moving approximately one hour more than on feeding days. Locomotion was generally higher during featherless chicken and meat-on-bone weeks, likely influenced by the heat cycle rather than differences between food items. Furthermore, enrichment positively affected locomotion, highlighting the importance of stimulation for zoo-housed felines. Locomotion increased with fasting duration, except for whole carcass feeding, where it dipped on day one before returning to feeding-day levels, likely due to prolonged satiation. A similar study in tigers also showed reduced movement on the first day after gorge feeding (Seyrling et al. 2024). These results also align with findings from Cavalcanti and Gese (2010), who found wild jaguars resumed hunting sooner after consuming smaller prey (1–15 kg, around three days between kills) compared to larger prey (30–45 kg, around five days between kills). These findings help explain why locomotion activity rebounded more quickly after smaller meals in the present study, while whole carcass feeding allowed for sustained inactivity. Evidently, large carcass feeding can thus contribute to structuring the activity of large predators on a scale beyond a single day.

Sleeping time significantly decreased on the second fasting day compared to a feeding day, with intermediate values on the first fasting day. This trend was consistent across all food items except whole carcass, where sleeping time remained stable, again likely due to prolonged satiation from larger meals. Similar effects were observed in Seyrling et al. (2024), where gorge feeding in tigers *Panthera tigris* increased post-feeding lying time. However, in that study, a longer fasting period (ten days) resulted in more pronounced behavioural shifts, highlighting how extended fasting intervals can alter activity budgets in ways that may differ from the shorter fasting periods employed in this study. Resting behaviour was less affected by food type and fasting, remaining consistent overall. Cold temperatures, however, reduced resting and increased sleeping, likely reflecting thermoregulatory adjustments.

Due to their repetitive nature, both anticipatory and stereotypic pacing were categorised as 'stereotypy' in the present study. The distinction between anticipatory pacing and stereotypic pacing is essential for understanding animal welfare (Watters 2014), but it is often impossible to conclude, in retrospect, which of these behaviours was recorded as 'pacing' in studies that did not make the distinction. Stereotypic pacing is often regarded as an indicator of compromised welfare and is perceived negatively by zoo visitors (Godinez et al. 2013). Anticipatory pacing, on the other hand, reflects heightened arousal and expectation, usually in response to predictable environmental cues, such as feeding routines or access to preferred areas (Watters 2014). Admittedly, the definition of anticipatory pacing may be problematic, and deciding whether a pacing event qualifies as anticipatory or non-anticipatory will require context (which is feasible under 24-h-observation). The welfare implications of anticipatory pacing remain debated. While some researchers consider it a positive sign of engagement and reward sensitivity, others view it as a potential expression of frustration or negative experiences (Watters 2014). This distinction has practical implications for animal management, as the underlying causes and solutions for the two behaviours can differ. Our study found that stereotypic pacing in jaguars remained largely unaffected by food items, fasting schedules, or environmental variables. This aligns with Morris (2018), who reported that 62% of jaguars in AZA institutions exhibited at least one stereotypic behaviour. Keepers could not identify triggers for these behaviours, though factors like high visitor density (conflicting results for jaguars: Sellinger and Ha 2005; Suárez et al. 2017) or cold temperatures have been suggested. Similarly, no clear links were found in this study.

Anticipatory pacing, however, was slightly elevated in winter, with jaguars pacing more near the indoor enclosure door on cold days (personal observation), consistent with observations by Stryker (2016) on thermoregulatory behaviour in felines. Anticipatory pacing increased on whole carcass feeding days. This likely resulted from the longer time required to suspend a whole carcass, extending the anticipatory period. Although fasting days were irregular, consistent keeper interactions sustained anticipatory pacing, making it independent of feeding schedules. Research suggests irregular feeding can reduce such behaviours by disrupting temporal cues (Shepherdson et al. 1993; Quirke et al. 2012; Seyrling et al. 2024). However, feeding-related cues, such as the smell of thawing meat, can still trigger this behaviour (Altman et al. 2005). These findings highlight the need to manage not only feeding schedules but also other predictable routines.

Our study emphasizes the impact of feeding different food items combined with a fasting regime on the behaviour and welfare of jaguars in ex-situ settings. Naturalistic feeding approaches, such as whole carcass provision followed by a fasting period, can help promote behaviours consistent with the species' ecological adaptations and encourage greater behavioural diversity. Whole carcasses not only prolonged feeding durations but also encouraged species-typical behaviours, such as carcass guarding and carrying, spreading consumption across several bouts including nocturnal feeding, and partitioning of the carcass into different parts, which were all less common with other food types. Additionally, they appeared to promote prolonged satiation, delaying the increase in locomotion typically observed after feeding and extending post-meal resting periods. While overall activity budgets for many behaviours remained stable and stereotypic pacing was largely unaffected, incorporating diverse, naturalistic feeding strategies that integrate enrichment into the feeding process may further enhance the welfare of zoo-housed carnivores.

Acknowledgements

We thank Marta Manser for support during the conduct of this project, and Matyas Liptovszky and an anonymous reviewer for comments on the manuscript. Conflict of interest: The authors declare no conflict of interest. The supplementary material is available on request from the corresponding author.

References

Altman J.D., Gross K.L., Lowry S.R. (2005) Nutritional and behavioural effects of gorge and fast feeding in captive lions. *Journal of Applied Animal Welfare Science* 8(1): 47–57. https://doi.org/10.1207/s15327604jaws0801_4

Anderson C., Von Keyserlingk M.A.G., Lidfors L.M., Weary D.M. (2020) Anticipatory behaviour in animals: A critical review. *Animal Welfare* 29(3): 231–238.

Andrews N.L., Ha J.C. (2014) The effects of automated scatter feeders on captive grizzly bear activity budgets. *Journal of Applied Animal Welfare Science* 17(2): 148–156.

Barbosa Santos A., Silverio R.A., Parolin L.C. (2020) The effect of visitation on the behaviour of captive individuals of *Panthera onca* (Linnaeus, 1758). *Mastozoología Neotropical* 27(1): 30–38.

Bashaw M.J., Bloomsmith M.A., Marr M.J., Maple T.L. (2003) To hunt or not to hunt? A feeding enrichment experiment with captive large felids. *Zoo Biology* 22(2): 189–198.

Bartoń K. (2025) MuMIn: Multi Model Inference. R package version 1.48.11, https://CRAN.R project.org/package=MuMIn

Bates D., Mächler M., Bolker B., Walker S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67(1): 1–48. doi:10.18637/jss.v067.i01.

Bond J.C., Lindburg D.G. (1990) Carcass feeding of captive cheetahs (*Acinonyx jubatus*): the effects of a naturalistic feeding program on oral health and psychological well-being. *Applied Animal Behaviour Science* 26(4): 373–382.

Brooks M.E., Kristensen K., van Benthem K.J., Magnusson A., Berg C.W., Nielsen A., Skaug H.J., Maechler M., Bolker B.M. (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal* 9(2): 378–400. doi:10.32614/RJ-2017-066

Cavalcanti S.M., Gese E.M. (2009) Spatial ecology and social interactions of jaguars (*Panthera onca*) in the southern Pantanal, Brazil. *Journal of Mammalogy* 90(4): 935–945.

Cavalcanti S.M., Gese E.M. (2010) Kill rates and predation patterns of jaguars (*Panthera onca*) in the southern Pantanal, Brazil. *Journal of Mammalogy* 91(3): 722–736.

Clauss M., Schiffmann C. (2023) Concepts of animal welfare in natural habitats and in zoos: Meaning and anxiety. In: Miller R.E., Calle P.P., Lamberski N. (eds.) *Fowler's Zoo and Wild Animal Medicine Current Therapy 10*. St Louis, MO: Elsevier, 255–260.

Clubb R., Mason G. (2003) Captivity effects on wide-ranging carnivores. *Nature* 425(6957): 473–474.

Crawshaw Jr P.G., Quigley H.B. (1991) Jaguar spacing, activity and habitat use in a seasonally flooded environment in Brazil. Journal of Zoology 223(3): 357–370.

De Cuyper A., Clauss M., Carbone C., Codron D., Cools A., Hesta M., Janssens G.P. (2019) Predator size and prey size–gut capacity ratios determine kill frequency and carcass production in terrestrial carnivorous mammals. *Oikos* 128(1): 13–22. https://doi.org/10.1111/oik.05488

Dobbins M.T., Steinberg M.K., Broadbent E.N., Ryan S.J. (2018) Habitat use, activity patterns and human interactions with jaguars *Panthera onca* in southern Belize. *Oryx* 52(2): 276–281..

EAZA (2022) *Best Practice Guidelines Jaguar (*Panthera onca*).* Amsterdam, Netherlands: EAZA Executive Office.

Emerson L.D., Wittmer H.U., Elbroch L.M., Kostoglou K., Bannister K.J., Psaila J.J., Whisson D., Ritchie E.G. (2025) A global assessment of large terrestrial carnivore kill rates. *Biological Reviews* 100(1): 327–350. https://doi.org/10.1111/brv.13143

Enemark L., Clauss M., Lagerström L., Burkevica A., Gustafsson J., Johnsson J., Lundgren P., Rhode H.L. (2023) The behavioural effects of feeding lean meat vs whole rabbit carcasses to zoo jaguars *Panthera onca. Journal of Zoo and Aquarium Research* 11(3): 324–328.

Friard O., Gamba M. (2016) BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution* 7(119): 1325–1330.

Garla R.C., Setz E.Z., Gobbi N. (2001) Jaguar (*Panthera onca*) food habits in Atlantic Rain Forest of southeastern Brazil. *Biotropica* 33(4): 691–696.

Godinez A.M., Fernandez E.J., Morrissey K. (2013) Visitor behaviours and perceptions of jaguar activities. *Anthrozoös* 26(4): 613–619.

Harmsen B.J., Foster R.J., Silver S.C., Ostro L.E., Doncaster C.P. (2011) Jaguar and puma activity patterns in relation to their main prey. *Mammalian Biology* 76(3): 320–324.

Hartig F. (2025). *DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models*. R package version 0.4.7, https://github.com/florianhartig/dharma

Hernández-Saint Martín A.D., Rosas-Rosas O.C., Palacio-Núñez J., Tarango-Arámbula L.A., Clemente-Sánchez F., Hoogesteijn A.L. (2013) Activity patterns of jaguar, puma and their potential prey in San Luis Potosi, Mexico. *Acta Zoológica Mexicana* 29(3): 520–533.

Jędrzejewski W., Cerda H., Viloria A., Gamarra J.G., Schmidt K. (2014) Predatory behaviour and kill rate of a female jaguar (*Panthera onca*) on cattle. *Mammalia* 78(2): 235–238.

Jędrzejewski W., Vivas I., Abarca M., Lampo M., Morales L.G., Gamarra G., Schmidt K., Hoogesteijn R., Carreño R., Puerto M.F., Viloria A.L., Breitenmoser C., Breitenmoser U. (2021) Effect of sex, age, and reproductive status on daily activity levels and activity patterns in jaguars (*Panthera onca*). *Mammal Research* 66: 531–539.

Jenny S., Schmid H. (2002) Effect of feeding boxes on the behavior of stereotyping Amur tigers (*Panthera tigris altaica*) in the Zurich Zoo, Zurich, Switzerland. *Zoo Biology* 21(6): 573–584.

Jeschke J.M. (2007) When carnivores are "full and lazy". *Oecologia* 152(2): 357–364.

Kassambara A. (2025). *ggpubr: 'ggplot2' Based Publication Ready Plots*. R package version 0.6.1, https://github.com/kassambara/ggpubr

Kleinlugtenbelt C.L.M., Clauss M., Burkevica A., De Cuyper A. (2023) Fasted and furious? Considerations on the use of fasting days in large carnivore husbandry. *Journal of Zoo and Aquarium Research* 11: 318-323

Krebs B.L., Chudeau K.R., Eschmann C.L., Tu C.W., Pacheco E., Watters J.V. (2022) Space, time, and context drive anticipatory behaviour: Considerations for understanding the behaviour of animals in human care. *Frontiers in Veterinary Science* 9: 972217.

Kroshko J., Clubb R., Harper L., Mellor E., Moehrenschlager A., Mason G. (2016) Stereotypic route tracing in captive Carnivora is predicted by species-typical home range sizes and hunting styles. *Animal Behaviour* 117: 197–209.

Lenth R., Piaskowski J. (2025). *emmeans: Estimated Marginal Means, aka Least-Squares Means*. R package version 2.0.0, https://CRAN.R-project.org/package=emmeans

Lyons J., Young R.J., Deag J.M. (1997) The effects of physical characteristics of the environment and feeding regime on the behaviour of captive felids. *Zoo Biology* 16(1): 71–83.

Maffei L., Cuéllar E., Noss A. (2004) One thousand jaguars (*Panthera onca*) in Bolivia's Chaco? Camera trapping in the Kaa-Iya National Park. *Journal of Zoology* 262(3): 295–304.

Mallapur A., Chellam R. (2002) Environmental influences on stereotypy and the activity budget of Indian leopards (*Panthera pardus*) in four zoos in Southern India. *Zoo Biology* 21(6): 585–595.

Mason G.J. (1991) Stereotypies: a critical review. *Animal Behaviour* 41(6): 1015–1037.

Mason G., Clubb R., Latham N., Vickery S. (2007) Why and how should we use environmental enrichment to tackle stereotypic behaviour? *Applied Animal Behaviour Science* 102(3–4): 163–188.

McPhee M.E. (2002) Intact carcasses as enrichment for large felids: Effects on on- and off-exhibit behaviours. *Zoo Biology* 21(1): 37–47.

Morris M.C. (2018) Treatment analysis of a captive male jaguar (*Panthera onca*). *UNF Graduate Theses and Dissertations* 799.

Núñez R., Miller B., Lindzey F. (2000) Food habits of jaguars and pumas in Jalisco, Mexico. *Journal of Zoology* 252(3): 373–379.

Podturkin A.A., Papaeva N. (2020) Development of an environmental enrichment programme: case study of white Bengal tiger (*Panthera tigris bengalensis*) and jaguar (*Panthera onca*) at Moscow Zoo. *Journal of Zoo and Aquarium Research* 8(2): 139–145.

Porfirio G., Sarmento P., Foster V., Fonseca C. (2017) Activity patterns of jaguars and pumas and their relationship to those of their potential prey in the Brazilian Pantanal. *Mammalia* 81(4): 401–404.

Quirke T., O'Riordan R.M., Zuur A. (2012) Factors influencing the prevalence of stereotypical behaviour in captive cheetahs (*Acinonyx jubatus*). *Applied Animal Behaviour Science* 142(3–4): 189–197.

Roller M., Müller D.W., Bertelsen M.F., Bingaman Lackey L., Hatt J.M., Clauss M. (2021) The historical development of juvenile mortality and adult longevity in zoo-kept carnivores. *Zoo Biology* 40(6): 588–596.

Schaller G.B., Vasconcelos J.M.C. (1978) Jaguar predation on capybara. *Mammalian Biology* 43: 296–301.

Schaller G.B., Crawshaw Jr P.G. (1980) Movement patterns of jaguar. *Biotropica* 12(3): 161–168.

Sellinger R.L., Ha J.C. (2005) The effects of visitor density and intensity on the behaviour of two captive jaguars (*Panthera onca*). *Journal of Applied Animal Welfare Science* 8(4): 233–244.

Seyrling I., Clauss M., Dierkes P.W., Burger-Schulz A.L. (2024) Breaking the spell: Changes in the behaviour of two zoo-kept tigers (*Panthera tigris*) after exposure to a distinct feast-and-fast feeding regime. *Zoo Biology* 43(4): 340–353.

Shepherdson D.J., Carlstead K., Mellen J.D., Seidensticker J. (1993) The influence of food presentation on the behaviour of small cats in confined environments. *Zoo Biology* 12(2): 203–216.

Stanton L.A., Sullivan M.S., Fazio J.M. (2015) A standardized ethogram for the felidae: A tool for behavioural researchers. *Applied Animal Behaviour Science* 173: 3–16.

Stark B. (2005) The use of carcass feeding to enhance animal welfare. In *Seventh International Conference on Environmental Enrichment*, New York, NY: Wildlife Conservation Society, 198–204.

Stryker J.A. (2016) Thermoregulatory behaviour assessment and thermal imaging of large felids. (Doctoral dissertation, University of Guelph).

Suárez P., Recuerda P., Arias-de-Reyna L. (2017) Behaviour and welfare: the visitor effect in captive felids. *Animal Welfare* 26(1): 25–34.

Vadret1.com. (2024) *Weather data and forecasts.* Retrieved from https://www.vadret1.com.

Veasey J.S. (2020) Can zoos ever be big enough for large wild animals? A review using an expert panel assessment of the psychological priorities of the Amur tiger (*Panthera tigris altaica*) as a model species. *Animals* 10: 1536.

Watters J.V. (2014) Searching for behavioural indicators of welfare in zoos: Uncovering anticipatory behaviour. *Zoo Biology* 33(4): 251–256.