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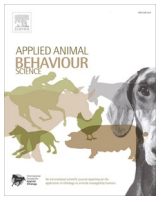

Effects of implementing a whole-carcass feeding routine on the behaviour of zoo-housed African lions (*Panthera leo*)

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ABSTRACT

The use of whole carcass feeding is common in large carnivore husbandry yet longer fasting intervals and their behavioural outcomes remain underexplored. This study examined behavioural changes in a small group of zoo-housed African lions (*Panthera leo*) at Monarto Safari Park following the introduction of a whole carcass feeding schedule. Seven lions were monitored: three adult males formed the test group and four lions (two males, two females) served as controls. The test group experienced a four-week baseline phase followed by an eight-week carcass-feeding phase in which a combined ~200 kg of kangaroo and goat carcasses was provided every nine days. Continuous 24-hour video allowed behaviour to be sampled at five-minute intervals across all phases. Feeding behaviour increased sharply on carcass days and displaced other active behaviours such as locomotion, while lying increased in the days following feeding. Pacing was higher in the second month of the experimental phase than in baseline and rose toward the end of each nine-day interval, suggesting increasing anticipation before feeding events. Hourly patterns showed consistent pacing peaks around typical shifting and feeding times. Overall, the whole-carcass feeding schedule altered activity across both months of the experimental phase and the six-day fasting interval, generating temporal patterns consistent with naturalistic feeding and post-feeding behaviour within this study group.

1. Introduction

African lions (*Panthera leo*) in the wild follow a natural feast-and-fast cycle shaped by the unpredictability of hunting success. After a successful hunt, lions can consume large quantities of meat in a single sitting (Schaller, 2009), often ingesting a substantial portion of their body weight before resting extensively to digest. Captive studies confirm that lions are adapted to irregular feeding and fasting cycles (Borstlap, 2002; Höttges et al., 2019). In the wild, they typically feed every 1.5–2.5 days but have been observed fasting for up to eight days (Eloff, 1984; Altman et al., 2005). Larger carnivores generally kill less frequently than smaller ones, reflecting the scaling of gut capacity and energy requirements. As body size increases, gut capacity grows disproportionately relative to metabolic rate, allowing large predators to ingest greater quantities at once and prolong the interval between hunts (De Cuyper et al., 2019). This allometric relationship underlies the natural feast-and-fast rhythm observed in many apex predators (Carbone et al., 1999; Jeschke, 2007). In lions, the combination of large stomach volume and high prey mass results in extended post-feeding rest and reduced feeding activity (Altman et al., 2005; Borstlap, 2002).

In zoos, however, feeding schedules are typically more frequent and predictable, with processed meat offered daily or near-daily (Clubb and Mason, 2007; Kleinlugtenbelt et al., 2023). While nutritionally adequate, these regimes differ from natural feeding ecology by reducing the variability, physical effort, and extended fasting periods characteristic of wild foraging cycles. Environmental enrichment is commonly used to reintroduce behavioural complexity into captive settings (Fernandez and Martin, 2021; Mellen and Sevenich MacPhee, 2001; Newberry, 1995; Waitt and Buchanan-Smith, 2001), and feeding-based enrichment is one approach to encourage species-typical feeding behaviours (Hosey et al., 2013; Hoy et al., 2010; Shepherdson et al., 1999). Whole carcass feeding, in particular, requires animals to tear, manipulate, and reposition prey items (McPhee, 2002; Bashaw et al., 2003), occupying them for longer periods and aligning more closely with

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natural predatory behaviour (Cremers et al., 2025; Enemark et al., 2023; Jordan et al., 2025). However, it is acknowledged that for obligate carnivores such as lions, which evolved to consume whole prey, providing carcasses could be argued to represent a core component of meeting biological and behavioural needs rather than an optional "extra" (Altman et al., 2005; Hayward and Hayward, 2007; Schaller, 2009). Given this, framing carcass feeding solely as enrichment risks lowering the perceived welfare baseline by implying that less natural feeding methods constitute an acceptable standard of care, rather than distinguishing between fundamental feeding requirements and additional forms of environmental stimulation (Young, 2013; Mellor, Beausoleil, 2015).

Previous research on carcass feeding in captive lions and other large carnivores has reported increases in feeding time, changes in activity budgets, and reductions in stereotypic pacing (Altman et al., 2005; Finch et al., 2020; Jenny and Schmid, 2002; McPhee, 2002; Jordan et al., 2025). However, many such studies were short in duration or focused primarily on the hours immediately following carcass provision (Finch et al., 2020; Jenny and Schmid, 2002), making it difficult to evaluate behavioural changes occurring during the fasting periods that follow. A recent long-term study by Seyrling et al. (2024) addressed this gap using 24-hour video over 104 days in tigers, demonstrating that behaviour can vary substantially across multi-day intervals following carcass ingestion. Most previous lion studies, however, provided partial carcasses or combined carcass feeds with regular meat portions (Altman et al., 2005; Brereton, 2020), limiting opportunities to assess behaviour across complete inter-feeding intervals. Management surveys further show that fasting and feeding practices vary widely across institutions (Kleinlugtenbelt et al., 2023), underscoring the need for detailed behavioural descriptions under different feeding schedules.

The present study investigated how African lions housed in a large safari park responded behaviourally to the introduction of a whole carcass feeding schedule involving longer intervals between feeds. Lions were monitored continuously over a three-month period encompassing both baseline and experimental phases, allowing 24-hour behavioural patterns to be quantified across multiple feeding cycles. During the experimental phase, lions were provided with whole kangaroo and goat carcasses totalling ~200 kg, which remained accessible for up to three days before approximately six days without food. This design enabled assessment of behaviour across both feeding and fasting periods rather than isolated feeding events. We predicted that feeding and locomotion would increase on carcass-access days due to the physical effort required to manipulate and consume intact prey, followed by increased resting during subsequent fasting days. Based on previous work, pacing was expected to decrease once carcass feeding was introduced, although changes were predicted to be correlated with study duration and inter-feeding interval. Together, this long-term, whole-of-day dataset provides insight into how lions adjust their behaviour under a carcass-feeding schedule that more closely resembles natural variability than typical zoo feeding regimes.

2. Methods

2.1. Ethics

All procedures in this study were conducted in accordance with the Australian Code for the Care and Use of Animals for Scientific Purposes (NHMRC, 2013) and the Animal Welfare Act 1995 (SA), as well as complying with Monarto Safari Park's animal welfare policies. The project was approved by Zoos South Australia Research Committee and the Adelaide University Animal Ethics Committee (S-2024–113). The study was non-invasive, and no physical interactions or handling of animals were required. All behavioural observations were conducted remotely via camera systems to minimise disturbance to the lions.

2.2. Location/subjects

This study was conducted at Monarto Safari Park (South Australia; 35.0880° S, 139.1625° E) between 10 February and 10 May 2025, corresponding to summer and early autumn in Australia. The subjects were seven African lions (*Panthera leo*), separated into two socially stable groups. The test group consisted of three adult males, all aged nine years, while the control group included four lions: two males aged three years and two females aged five years.

The lions were housed in three enclosures with natural substrate and enrichment features such as trees and logs. The on-exhibit habitat was approximately 10.27 ha, while the two off-exhibit holding areas had an approximate area of 105 m^2. The two study groups were housed in adjacent enclosures, separated by a weld mesh fence and a physical gap between the boundaries, allowing for potential visual, auditory, and olfactory contact. For the purposes of public viewing and animal management, the lions were rotated through the primary visitor-accessible habitat throughout the day. The control group was typically on exhibit between 09:00 and 15:00–16:00 and participated in public *Lions 360* feeding encounters, whereas the test group was generally housed in the public exhibit overnight.

2.3. Equipment

To enable 24 h behavioural monitoring, eight GardePro A60 4 K (non-cellular) infrared cameras (Shenzhen Zhuopu Digital Technology Co. Ltd, Shenzhen City, China) were installed across the three on-exhibit and off-exhibit enclosures. Six cameras were positioned in the main exhibit and two in the off-exhibit night yards or holding areas not accessible to visitors (Fig. 1). Cameras were mounted using zip ties and positioned to maximise coverage of key areas such as resting sites, feeding locations, and pathways. Areas not visible to the cameras, primarily portions of the main exhibit obscured by topography, are shown in Fig. 1, which illustrates both camera placement and associated visibility zones. Camera placement was planned collaboratively with the keeper team, who assisted in identifying the areas most frequently used by the lions; the cameras were installed together with keepers to ensure that high-use spaces such as resting sites, paths, and feeding zones were prioritised for visibility. Each camera recorded 10-second clips every 5 min, 24 h a day, 7 days a week, for the duration of the study. SD cards were swapped weekly as they approached capacity, and video data were transferred to a 1 TB external hard drive for secure storage and later analysis.

To monitor feeding, carcasses were weighed on a digital scale prior to introduction. After feeding events, any uneaten remains were removed and weighed, with bone weight subtracted to estimate actual consumption, primarily for husbandry and health monitoring rather than for use as an outcome measure in the behavioural analyses.

2.4. Study design

The study involved a carcass-feeding intervention applied to the test group, while the control group continued to be fed the facility's standard diet. The test group's 12-week schedule began with a 4-week baseline period, followed by an 8-week carcass-feeding phase. During the carcass phase, whole kangaroo or goat carcasses (totalling approximately 200 kg per feed) were provided every nine days for two to three days, followed by six to seven days of fasting. Feeding events typically occurred between 09:00 and 10:00, and carcasses remained in the enclosure for up to three days to allow for naturalistic consumption.

During the baseline phase, the test group lions were occasionally shifted into the larger on-exhibit enclosure during visiting hours (approximately 09:00–16:00) and returned to their smaller off-exhibit enclosure overnight. Additionally, during this phase, the test group received their standard diet, which consisted of horse, deer, rabbit, turkey, and pig provided primarily as cut portions or partial carcass

Fig. 1. Satellite image of the African lion (Panthera leo) habitat at Monarto Safari Park, South Australia. The primary visitor-facing exhibit (10.27 ha) and off-exhibit holding areas (105 m^2) are shown. Locations of the eight infrared GardePro A60 4 K cameras used for 24-h behavioural monitoring are indicated, with six in the main exhibit (red camera icons) and two in the off-exhibit enclosures (green camera icons). Shaded regions denote areas not visible to the cameras.

sections, with occasional whole small prey items (e.g. defeathered poultry), rather than as large intact carcasses presented as a single feeding event. This differed from the carcass-feeding phase, in which complete kangaroo or goat carcasses were provided whole and consumed over multiple days.

During the carcass-feeding phase, enclosure use was modified to accommodate the feeding schedule and to exclude the lions from public feedings. Carcasses were presented in the off-exhibit enclosure in the morning, and the lions remained there for the duration of carcass access (two to three days). After the carcass was removed, typically on the third morning or evening, the lions were shifted to the on-exhibit enclosure overnight for the subsequent fasting period and returned to the off-exhibit area during the day once keepers arrived (09:00–10:00).

These changes in enclosure access occurred as part of standard management procedures and were not a deliberate component of the experimental design. Because visibility was reduced at night in the larger on-exhibit enclosure, and because certain topographic and vegetated areas were not consistently camera-covered, some behaviours could occur out of sight. Since carcasses were always provided in the smaller off-exhibit enclosure, feeding behaviour was consistently visible to the cameras, whereas behaviours such as resting, lying down, locomotion, and pacing could occur out of sight when animals moved into the larger enclosure (Fig. 1).

The control group maintained their regular feeding schedule throughout the study, being fed five times per week at approximately 11:00, 13:00, or 15:00, depending on husbandry needs and whether a *Lions 360* visitor interaction occurred that day. Off-exhibit feeds were conducted by keepers using a feeding chute or access door, providing meat items such as horse, kangaroo, or pig as portions or partial carcass sections rather than as large intact carcasses. When the lions were on exhibit, small portions of meat were offered during the *Lions 360* visitor interaction, in which guests entered a protected caged dome within the exhibit while keepers encouraged the lions to approach and climb onto the structure. These encounters occurred approximately every two days, usually around 10:40 or 12:50, with some visitors feeding the lions under keeper supervision. Feeding logs recorded the type, weight, and time of each feed, ensuring consistent monitoring of diet across the study.

2.5. Behavioural observations

Behavioural data were collected via 24 h video recording over the three-month study period using eight cameras. For simplicity, the term ‘day’ is used throughout to denote a full 24-hour period. Video footage

was sampled using instantaneous pinpoint scan sampling (Altmann, 1974; Bateson and Martin, 2021) at 5-minute intervals, 24 h per day, 7 days per week, producing a high-resolution dataset spanning both day and night. Behavioural data were expressed as percentages rather than counts to account for differences in group sizes between the test and control groups, allowing direct comparison of proportional engagement in each behaviour. Percentages represented the proportion of instantaneous pinpoint scans in which a behaviour occurred over all total instances within a one-hour session. For example, if two lions in a three-lion group were observed pacing four times each within an hour (8 instances total) this would be divided by the total number of lions (3 individuals) multiplied by possible instances of behaviour (12 5-minute scans), therefore resulting in 8 responses divided by 36, or 0.222 (22.2%).

An ethogram (Table 1) was used to record a range of behaviours with operational definitions adapted from established lion and felid ethograms (Schaller, 2009; Jenny and Schmid, 2002; Clubb and Mason, 2007; Stanton et al., 2015). Two observers were trained together using shared video samples to ensure consistent application of behavioural definitions. Inter-observer agreement (IOA) was calculated using the total agreement method (Poling et al., 1995), defined as the smaller count divided by the larger count for each behaviour class within each hourly observation session, multiplied by 100.

Because individual identities could not reliably be distinguished on camera, behaviours were recorded at the group level. For each 5-minute timepoint, the presence of a behaviour from any individual in the group was scored. Percentages were calculated for each behaviour within daily and hourly timeframes to assess temporal trends and treatment effects.

Table 1
Ethogram of behaviours, their definitions, and the classes to which they were attributed. Behaviours were separated in 5 classes: active, inactive, social, abnormal and other.

Behaviour	Definition	Class
Locomotion	Directed non-repetitive movement	Active
Manipulating Object	Contact with a non-edible object, with any part of the body manipulating its position	Active
Feeding	Cat interacts with and/or ingests food by means of chewing with the teeth and swallowing.	Active
Lying Down	Cat's body is on the ground in a horizontal position, including on its side, back, belly, or curled in a circular formation.	Inactive
Sitting	Cat is in an upright position, with the hind legs flexed and resting on the ground, while front legs are extended and straight	Inactive
Standing	Cat is in an upright position and immobile, with all four paws on the ground and legs extended, supporting the body.	Inactive
Social - Affiliative	Social play (play-fight, chasing, playing together with an enrichment device), putting the front paw or rubbing on a conspecific, social grooming (licking a conspecific or being licked)	Social
Social - Agonistic	Dominance mount, threat display, aggression	Social
Vocalization (visible)	Lion is visibly engaging in vocal behaviour (open mouth, extended neck and repeated jaw movements)	Social
Pacing	Repetitive locomotion in a fixed pattern, such as back and forth along the same route. Movement seems to have no apparent goal or function. Must be performed for at least 10 s.	Abnormal
Repetitive - Other	Self-inflicting repetitive behaviours, including fur plucking, head-rolling and over-grooming.	Abnormal
Out of Sight	Cat is not visible to the observer	Other
Urinate/Defecate	Cat releases faeces on the ground while in a squatting position or Cat releases urine on the ground while in a squatting position.	Other
Autogroom	Cat cleans itself by licking, scratching, biting or chewing the fur on its body. May also include the licking of a front paw and wiping it over one's head.	Other
Other	Any other behaviour	Other

These percentages represent the proportion of instantaneous scans in which a behaviour occurred within an hour, averaged across all hours in a day, and subsequently averaged across the study phase or cycle grouping. The use of proportions reflects this group-level scoring approach and avoids artefacts associated with group size, meaning that results represent collective temporal patterns rather than individual behavioural investment.

All behavioural data were collected using the ZooMonitor app (version 1.7.140; Lincoln Park Zoo, Chicago, IL, USA) and later exported to Excel for analysis in R (Version 4.4.1).

2.6. Statistical analysis

All statistical analyses were conducted in R (Version 4.4.1; R Core Team., 2024). For the baseline comparison between the test and control groups, behaviour was averaged by day to produce daily means, which were compared using independent-sample *t*-tests for each broad behavioural class (Jenny and Schmid, 2002). This approach provided a general overview of group-level differences prior to the experimental phase.

For within-test-group analyses (i.e., month-to-month and cycle-day comparisons), behaviour was averaged by hour to capture finer-scale variation across the feast–fast cycle. Each hour represented a distinct sampling unit, with values reflecting the percentage of scans in which a behaviour occurred within that hour.

Linear mixed models (LMMs) were fitted for each behaviour using the *lmer* function from the *lmerTest* package in R (Fernandez et al., 2025). Separate models were constructed to examine (1) differences across Month (Baseline, Month 1, Month 2) and (2) differences across cycle-day groupings (Days 1–3 [feeding], Days 4–6 [mid-fast], Days 7–9 [late-fast]). In all models, Month or Cycle Day Group was specified as a fixed effect, and Date was included as a random effect to account for repeated measures across days.

Model assumptions were evaluated by visual inspection of residual and Q–Q plots. Although the data violated tests of normality, LMMs were used due to their robustness to non-normal residuals under moderate to large sample sizes (Bolker et al., 2009; Ghasemi and Zahediasl, 2012), and their widespread use in studies of captive carnivore behaviour (Kroshko et al., 2016). When main effects were significant, Tukey-adjusted post-hoc comparisons were performed using the *emmeans* package in R to identify differences between months or cycle-day groupings (Höttges et al., 2019; Brando and Buchanan-Smith, 2018). An alpha level of 0.05 was adopted for all tests.

3. Results

Inter-observer agreement (IOA) was calculated for all behaviour classes across sessions scored by both observers, representing 23.5% of all observation sessions. Mean IOA exceeded 97% across all classes, ranging from 97.2% for Active behaviours to 99.1% for Other behaviours. Most individual sessions for each behaviour class showed agreement between 80% and 100%, with only a small proportion of sessions (5.0% of Abnormal, 4.3% of Active, 1.2% of Inactive, 2.3% of Social, and 0.4% of Other behaviours) falling below the 80% threshold. These lower-agreement sessions primarily reflected periods in which very few instances of the behaviour were recorded (i.e., fewer than five occurrences per session).

3.1. Test vs. control groups

During the baseline phase, the control and test groups differed significantly across several behavioural classes (Fig. 2). The test group spent substantially less time inactive than the control group, $t(55) = 7.27$, $p < 0.001$, 95% CI = [17.7, 31.1]. In contrast, the test group showed more Active behaviour, $t(55) = -2.90$, $p = 0.005$, 95% CI = [−1.37, −0.25], and more Other behaviour, $t(55) = -6.78$,

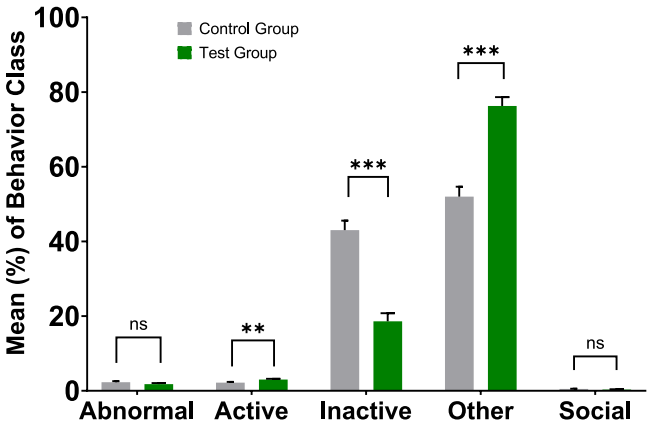

Fig. 2. Baseline mean (± SE) percentage of time spent in each behavioural class for the control group (grey) and test group (green). Percentages reflect the average proportion of instantaneous scans in which a behavioural class occurred. Asterisks denote Welch *t*-test results for between-group differences ($p < 0.05$ = *, $p < 0.01$ = **, $p < 0.001$ = ***; ns = not significant).

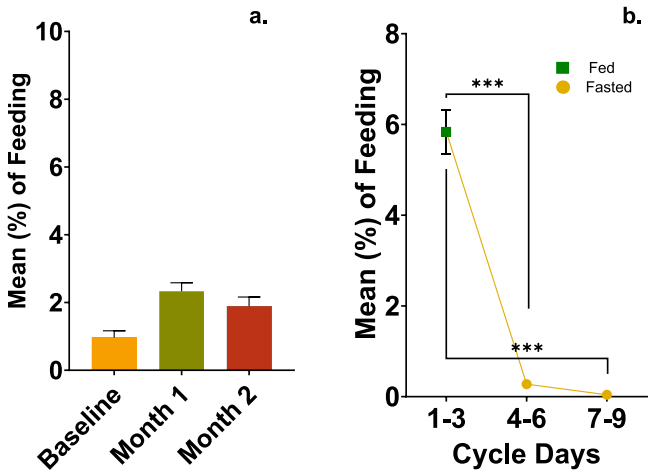

Fig. 3. Mean (± SE) percentage of time spent feeding by the test group of African lions during (a) the baseline phase, month 1, and month 2 of the carcass feeding period, and (b) across the nine-day carcass feeding cycle, grouped into days 1–3, 4–6, and 7–9. Percentages represent the average proportion of instantaneous scans in which feeding occurred. Asterisks indicate significant differences between groups from Tukey post-hoc comparisons ($p < 0.001$ = ***).

$p < 0.001$, 95% CI = [−31.5, −17.1], than the control group. Abnormal behaviour did not differ significantly between groups, $t(55) = 1.30$, $p = 0.20$, 95% CI = [−0.28, 1.32], nor did Social behaviour, $t(54) = 1.62$, $p = 0.11$, 95% CI = [−0.04, 0.36]. (CIs are for the mean difference Control − Test; negative values indicate higher values in the test group.)

Given that baseline behaviour differed significantly between groups for most behavioural classes, we did not conduct further between-group comparisons during the experimental phase. These baseline differences may partially reflect underlying differences in group composition, including age and sex structure, which further limited the suitability of direct between-group comparisons during the experimental phase. Instead, subsequent analyses examined within-group changes across the carcass feeding and fasting cycles (within the test group), as comparing groups with different starting points would not provide a meaningful assessment of changes related to the carcass-feeding treatment.

3.2. Within-test group differences

3.2.1. Feeding

Feeding did not vary across months during the study ($F(2, 87.0) = 2.26$, p=0.11; Fig. 3a). Although the overall effect was not significant, post-hoc comparisons indicated that feeding tended to be higher in Month 1 (2.33 ± 0.45%) than in the baseline period (0.97 ± 0.47%; $t(87) = 2.10$, p=0.097). Feeding in Month 2 (1.89 ± 0.47%) did not differ significantly from either baseline ($t(87) = 1.38$, p=0.36) or Month 1 ($t(87) = 0.68$, p=0.78).

There was a significant effect of cycle day grouping on feeding behaviour during the carcass-feeding phase ($F(2, 1459) = 124.68$, $p < 0.001$; Fig. 3b). Feeding was highest on Days 1–3 immediately following carcass provision (5.84 ± 0.29%) and declined sharply across the fasting period. Specifically, feeding was higher on Days 1–3 than on Days 4–6 ($t(58) = 13.50$, $p < 0.001$) and Days 7–9 ($t(58) = 13.73$, $p < 0.001$), with no difference between Days 4–6 and Days 7–9 ($t(58) = 0.55$, p=0.85).

To further characterise feeding behaviour during the carcass-feeding phase, several descriptive metrics were calculated for the experimental group (Fig. 4). Across all carcass days (n = 7), lions spent substantially more time feeding than during baseline, averaging 76.4 ± 35.2 min per day compared with 25.7 ± 30.3 min at baseline ($t(34) = 3.86$, $p < 0.001$; Wilcoxon W = 22.5, $p = 0.0016$). The number of daily feeding bouts also increased, from 5.2 ± 3.1 bouts per day at baseline to 11.8 ± 4.6 on carcass days. Individual feeding bouts averaged 7.4 ± 2.8 min in duration (range 5–20 min), and total feeding span, the interval between the first and last feeding scan, extended up to 3 h 35 min following carcass presentation. Latency to begin feeding averaged 16.4 ± 17.2 min.

Concurrent feeding was also more common during carcass access. The mean number of simultaneous feeders increased from 0.04 ± 0.05 at baseline to 0.60 ± 0.45 on carcass days ($t(34) = 6.91$, $p < 0.001$; Wilcoxon W = 3, $p < 0.001$). Similarly, the proportion of scans in which two or more lions were feeding rose from 1.2 ± 1.5% at baseline to 19.0 ± 17.5% during carcass feeding ($t(34) = 5.65$, $p < 0.001$; Wilcoxon W = 29, $p = 0.0035$).

3.2.2. Locomotion

Locomotion did not vary significantly across months ($F(2, 87.1) = 3.18$, p=0.047; Fig. 5a). Although the model showed a small trend, none of the pairwise comparisons were significant after Tukey adjustment for multiple comparisons. Locomotion in Month 1 (2.62 ± 0.20%) was slightly higher than in the baseline period (2.01 ± 0.21%), but this difference was not significant ($t(87) = 2.17$, p=0.083). Month 2 (2.01 ± 0.21%) did not differ from either baseline ($t(87) = 0.00$, p=1.00) or Month 1 ($t(87) = 2.16$, p=0.083).

In contrast, there was a significant effect of cycle day grouping on locomotion ($F(2, 57.9) = 10.19$, $p < 0.001$; Fig. 5b). Locomotion was lowest immediately after feeding (Days 1–3 = 1.53 ± 0.24%) and increased mid-cycle (Days 4–6 = 3.08 ± 0.24%), remaining slightly elevated at the end of the cycle (Days 7–9 = 2.39 ± 0.26%). Post-hoc Tukey comparisons indicated locomotion was significantly higher on Days 4–6 than Days 1–3 ($t(58) = -4.51$, $p < 0.001$) and on Days 7–9 than Days 1–3 ($t(58) = -2.44$, p=0.046), with no difference between Days 4–6 and 7–9 ($t(58) = 1.95$, p=0.133).

3.2.3. Pacing

Pacing varied significantly across months ($F(2, 87.0) = 4.51$, p=0.014; Fig. 6a). Post-hoc Tukey comparisons showed that pacing was significantly higher in Month 2 (3.83 ± 0.48%) than during the baseline phase (1.79 ± 0.48%; $t(87) = -3.00$, p=0.0097). Pacing during Month 1 (2.76 ± 0.46%) did not differ significantly from either baseline (p=0.315) or Month 2 (p=0.245). These results indicate a gradual increase in pacing over the carcass-feeding period, reaching its highest level by Month 2.

There was no significant effect of cycle day grouping on pacing behaviour ($F(2, 58.0) = 1.85$, $p = 0.17$; Fig. 6b). Pacing showed limited variation across the nine-day feeding cycle, with a small, non-significant

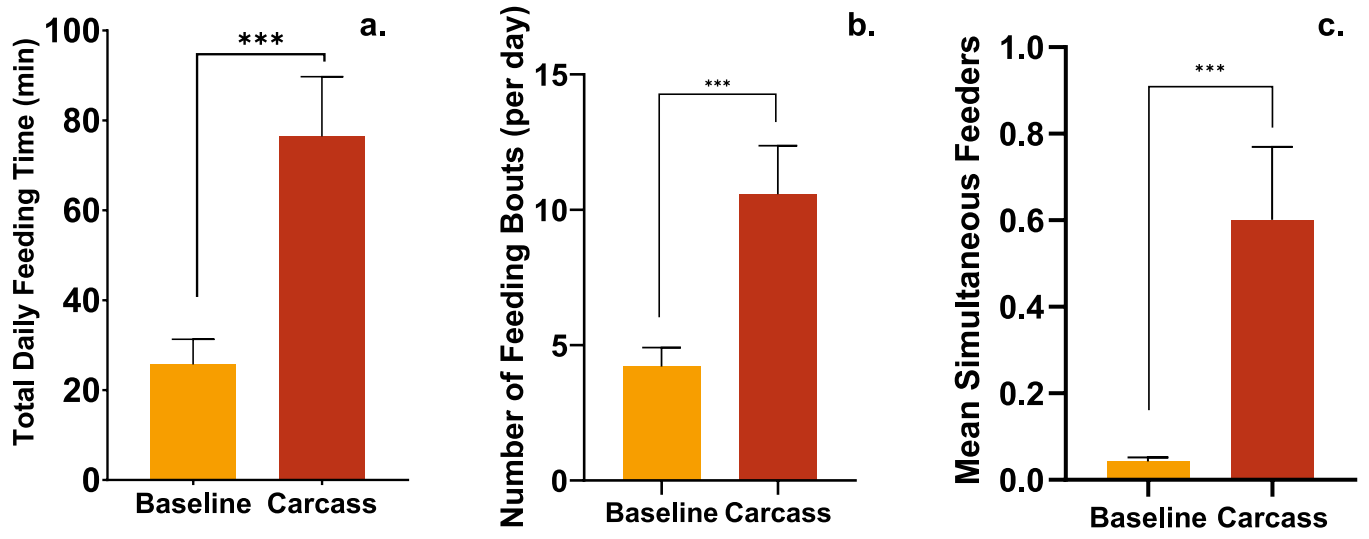

Fig. 4. Feeding behaviour of the test-group lions during baseline and carcass-feeding days.(a) Total daily feeding time (min), representing the sum of all 5-min scan samples in which at least one lion was recorded feeding.(b) Number of feeding bouts per day, calculated as discrete feeding events separated by at least one non-feeding scan.(c) Mean number of simultaneous feeders, representing the average number of lions feeding at the same time across all scans each day. Bars show mean ± SE across all baseline days and all carcass-feeding days. Carcass days consisted of whole kangaroo and goat carcasses provided for 2–3 days per feeding cycle. Asterisks indicate significant differences between conditions (*** p<0.001).

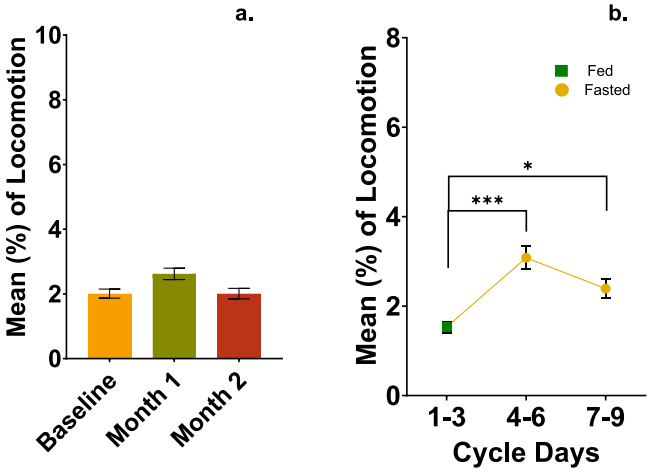

Fig. 5. Mean (± SE) percentage of time spent in locomotion by the test group of African lions during (a) the baseline phase, month 1, and month 2 of the carcass feeding period, and (b) across the nine-day carcass feeding cycle, grouped into days 1–3, 4–6, and 7–9. Percentages represent the proportion of instantaneous scans in which locomotion occurred, averaged per day. Asterisks indicate significant differences between baseline and carcass phases within each cycle day grouping from Tukey post-hoc comparisons ($p < 0.05$ = *, $p < 0.001$ = ***).

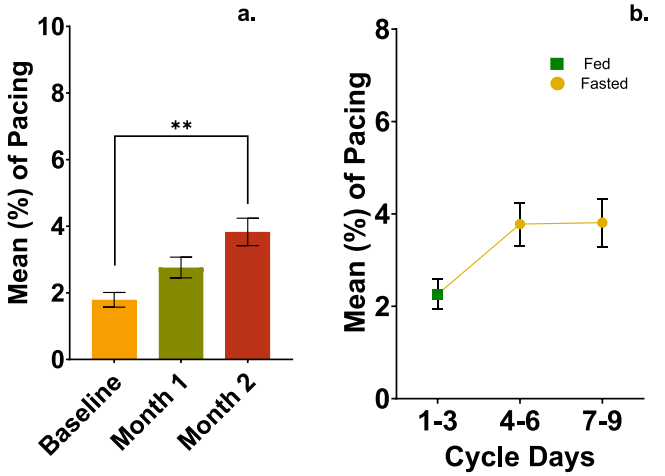

Fig. 6. Mean (± SE) percentage of time spent pacing by the test group of African lions during (a) the baseline phase, month 1, and month 2 of the carcass feeding period, and (b) across the nine-day carcass feeding cycle, grouped into days 1–3, 4–6, and 7–9. Percentages represent the proportion of instantaneous scans in which pacing occurred, averaged per day. Asterisks indicate significant differences between baseline and carcass phases within each cycle day grouping from Tukey post-hoc comparisons (p<0.01 = **).

increase toward the end of the fasting period. Mean pacing was 2.26 ± 0.65% on Days 1–3, 3.78 ± 0.65% on Days 4–6, and 3.81 ± 0.68% on Days 7–9. No significant differences were detected between cycle day groupings (all $p > 0.23$), indicating that pacing did not differ systematically across the feast–fast cycle.

To further explore temporal structure in pacing behaviour, we plotted hourly pacing across the 24-hour day for each cycle day grouping (Days 1–3, 4–6, 7–9; Fig. 7). Although the mixed-model analysis did not detect significant differences between cycle day groups, the descriptive hourly patterns revealed two consistent peaks: one in the morning (around 09:00–10:00) and another in the late afternoon (around 15:00–16:00). These peaks coincided with routine keeper arrival and shifting times, and—on Day 1—also with carcass presentation. Pacing increased modestly during the late fasting period (Days 7–9), consistent with the month-level rise observed in Month 2, although these differences did not reach statistical significance at the hourly scale.

3.2.4. *Lying down*

Lying down varied significantly across months ($F(2, 87.0) = 9.59$, $p < 0.001$; Fig. 8a). Post-hoc Tukey comparisons indicated that lions spent significantly more time lying down during Month 1 (34.9 ± 3.25%) and Month 2 (32.8 ± 3.42%) of the carcass-feeding phase than during the baseline period (15.8 ± 3.42%). The increase from baseline to Month 1 was significant ($t(87) = -4.05$, $p < 0.001$), as was the increase from baseline to Month 2 ($t(87) = -3.51$, $p = 0.002$). No difference was detected between Month 1 and Month 2 ($t(87) = 0.45$, $p = 0.895$).

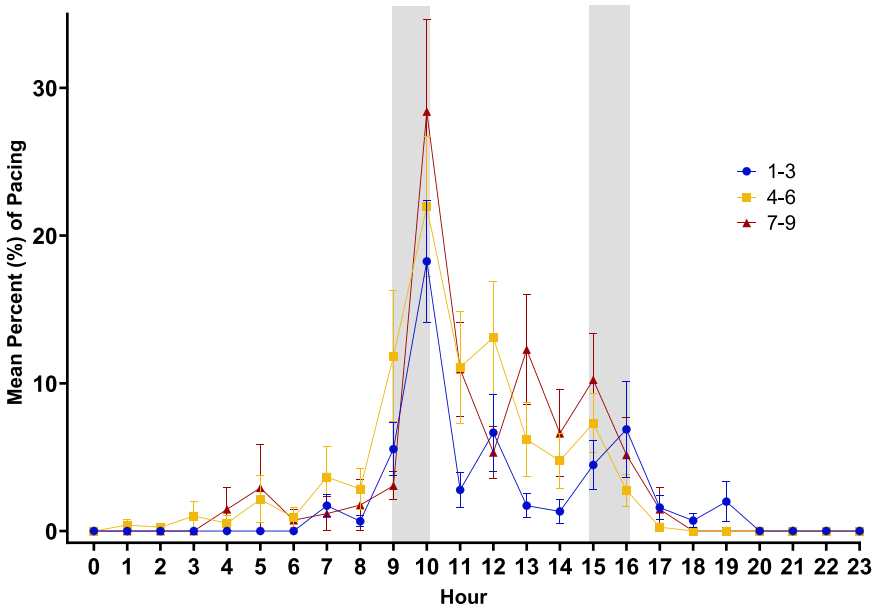

Fig. 7. Hourly pacing behaviour of the test-group lions across the 9-day carcass-feeding cycle. Mean ± SE percentage of pacing is plotted for each hour of the day, separated into three cycle-day groups: Days 1–3 (immediately following carcass provision), Days 4–6 (mid-fast), and Days 7–9 (late-fast). Percentages represent the proportion of 5-min scan samples within each hour in which at least one lion was observed pacing. Grey shaded bands indicate routine keeper-directed enclosure shifts (approx. 09:00–10:00 and 15:00–16:00), during which pacing commonly increased. This figure illustrates how pacing intensity varies both diurnally and across the feeding–fasting sequence.

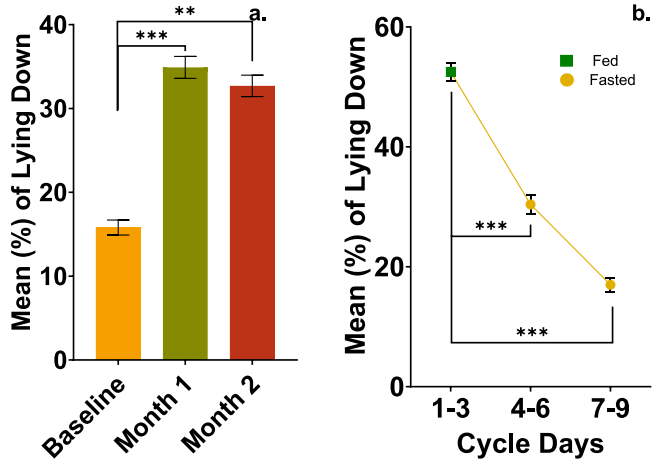

Fig. 8. Mean (± SE) percentage of time spent lying down by the test group of African lions during (a) the baseline phase, month 1, and month 2 of the carcass feeding period, and (b) across the nine-day carcass feeding cycle, grouped into days 1– 3, 4–6, and 7–9. Percentages represent the proportion of instantaneous scans in which lying down occurred, averaged per day. Asterisks indicate significant differences between baseline and carcass phases within each cycle day grouping from Tukey post-hoc comparisons (p<0.01 = **, p<0.001 = ***).

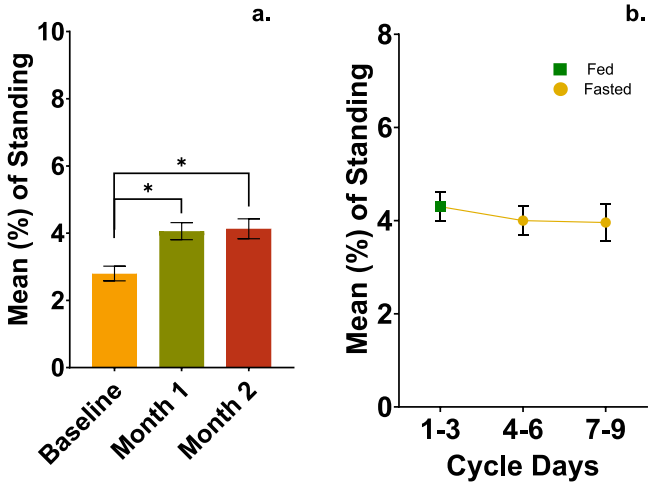

Fig. 9. Mean (± SE) percentage of time spent standing by the test group of African lions during (a) the baseline phase, month 1, and month 2 of the carcass feeding period, and (b) across the nine-day carcass feeding cycle, grouped into days 1–3, 4–6, and 7–9. Percentages represent the proportion of instantaneous scans in which standing occurred, averaged per day. Asterisks indicate significant differences between baseline and carcass phases within each cycle day grouping from Tukey post-hoc comparisons (p<0.05 = *).

There was also a significant effect of cycle day grouping on lying down behaviour ($F(2, 58.0) = 27.86$, $p < 0.001$; Fig. 8b). Lying down was highest immediately after feeding (Days 1–3 = 52.5 ± 3.32%) and declined steadily across the fasting period (Days 4–6 = 30.4 ± 3.33%, Days 7–9 = 17.0 ± 3.49%). Post-hoc comparisons showed that lions spent significantly more time lying down on Days 1–3 than on Days 4–6 ($t(58) = 4.68$, $p < 0.001$) and Days 7–9 ($t(58) = 7.36$, $p < 0.001$), and more on Days 4–6 than Days 7–9 ($t(58) = 2.80$, $p = 0.019$).

3.2.5. Standing

Standing varied significantly across months ($F(2, 87.1) = 4.95$, $p = 0.009$; Fig. 9a). Post-hoc Tukey comparisons indicated that standing increased significantly from the baseline period (2.80 ± 0.34%) to Month 1 (4.06 ± 0.32%; $t(87) = -2.70$, $p = 0.023$) and to Month 2 (4.13 ± 0.34%; $t(87) = -2.77$, $p = 0.019$). No significant difference was detected between Month 1 and Month 2 ($t(87) = -0.14$, $p = 0.989$).

There was no significant effect of cycle day grouping on standing behaviour ($F(2, 58.1) = 0.20$, $p = 0.82$; Fig. 9b). Standing remained consistent across the feast–fast cycle, with means of 4.30 ± 0.41% on Days 1–3, 4.00 ± 0.41% on Days 4–6, and 3.96 ± 0.43% on Days 7–9. No significant pairwise differences were found between cycle day groupings (all $p > 0.83$).

4. Discussion

This study examined how a whole-carcass feast–fast feeding schedule impacted the behaviour of African lions across the full 24-hour day and over repeated nine-day cycles. Continuous behavioural sampling revealed structured temporal patterns linked to carcass availability, fasting, and routine husbandry events. Whole-carcass access produced prolonged feeding bouts extending across day and night, followed by increased resting, while fasting days were characterised by gradual increases in locomotion and anticipatory behaviours near typical management times. Pacing showed temporal association with keeper arrival rather than progressive escalation across the fasting interval, and no increase in aggression or social instability was observed around carcasses. Together, these findings indicate that both the feeding schedule and patterns of enclosure use influenced activity, rest, and pre-feeding behaviour over multi-day timescales.

Whole-carcass access produced clear increases in feeding behaviour on carcass days, with lions engaging in extended bouts and returning to the carcass intermittently throughout the day and night. These prolonged feeding periods reflect the handling demands of whole prey and align with natural feeding patterns in wild lions, which consume large meals over extended periods when available (Schaller, 2009; Altman et al., 2005). Anecdotally, the three males typically separated themselves during feeding, each selecting a carcass and feeding alone rather than cooperating to tear or share portions, consistent with the well-documented pattern in which cooperative hunting does not translate into cooperative feeding (Schaller, 2009). The lions generally stayed near the carcasses, indicating that carcass presence strongly anchored space use. As carcasses were depleted over two to three days, feeding shifted from sustained handling on Day 1 to shorter, opportunistic bouts on subsequent days.

Although the present study focused on behavioural outcomes rather than direct welfare assessment, the findings can be considered within a broader welfare framework. The Five Domains model emphasises the interaction between physical state (e.g., nutrition) and opportunities for species-typical behaviour in shaping overall mental state (Mellor, Beausoleil, 2015). Whole carcass feeding alters not only the nutritional form of food but also its presentation, requiring tearing, repositioning, and extended handling. These characteristics more closely resemble aspects of natural feeding ecology and are consistent with behavioural expressions associated with predation and post-feeding rest. At the same time, the use of "naturalness" as a welfare metric remains debated, and behavioural change alone cannot be assumed to reflect improved welfare. Accordingly, the present findings should be interpreted as documenting structured behavioural responses to feeding regime rather than empirically demonstrating welfare enhancement, although this possibility would require further evaluation using a multi-dimensional approach.

Behaviour varied systematically across the nine-day cycle. Following carcass provision, lying down increased and locomotion decreased, reflecting both the physical effort of feeding and post-feeding rest associated with large, fibrous meals (Law and Kitchener, 2020). As fasting progressed, locomotion increased, particularly toward Days 7–9, mirroring ecological patterns in which wild lions alternate between intensive feeding and extended periods of reduced activity interspersed with searching or waiting (Hayward and Hayward, 2007; Schaller, 2009). These results highlight that even in zoos, feeding schedule structure can generate predictable temporal rhythms in behaviour.

Pacing and standing provided insight into how lions responded to predictable management routines. Because pacing was quantified at the group level, these patterns reflect collective activity rather than individual stereotypic expression. Pacing increased between baseline and the second month of carcass feeding but did not differ significantly across the nine-day feeding cycle and remained lowest on feeding days. Peaks occurred near routine husbandry and feeding times, consistent with anticipatory behaviour associated with predictable events rather than with a progressive increase driven by prolonged fasting. Although pacing is often interpreted as a stereotypic behaviour in captive carnivores, its temporal structure in this study, characterised by time-of-day clustering and the absence of escalation across fasting days, suggests a situational response linked to management cues (Fernandez, 2021; Harst and Spruijt, 2007; Mason and Latham, 2004). Importantly, no increase in aggression or social instability was observed during carcass access, and interactions around carcasses remained stable throughout the study. It was not possible within the current ethogram to distinguish pacing from other forms of repetitive or potentially goal-directed locomotion (e.g., patrolling), which may be relevant for interpreting increased movement in later fasting stages and should be considered in future studies.

Patterns of visibility and "out of sight" behaviour must be interpreted in relation to enclosure allocation rather than as indicators of withdrawal or reduced activity. During baseline, lions spent part of each day on exhibit and were returned off-exhibit overnight, whereas during carcass access they remained off-exhibit for extended periods while feeding occurred. As a result, periods coded as "out of sight" largely reflected physical enclosure location rather than changes in motivation or engagement. Detailed analyses of visibility patterns are presented in Appendix 1 to support interpretation of these effects without detracting from the primary behavioural results.

The extensive 24-hour monitoring used here provided several methodological advantages. Many zoo-based studies rely on short daytime observation windows, which can miss nocturnal feeding, post-feeding rest, and shifts in activity occurring before or after keeper arrival (Mason et al., 2007). Instantaneous scans every five minutes across three months allowed subtle temporal changes, including early-morning anticipation and late-night feeding, to be captured with precision. Similar high-resolution monitoring in other carnivores has shown that long-term, continuous sampling provides a more accurate picture of behavioural cycles than daytime-only methods (Beer et al., 2024; Weller and Bennett, 2001).

Several limitations should be acknowledged. The test group consisted of three adult males, while the control group included both males and females, and differed in age structure. These differences in group composition may have contributed to the baseline behavioural differences observed between groups, which precluded meaningful between-group comparisons during the experimental phase. As a result, conclusions are based on within-group changes in the test group under the carcass-feeding regime rather than direct contrasts with the control group. This limits generalization to other social structures, such as mixed-sex groups or prides.

Because the test group could not participate in public feeding encounters during fasting, their enclosure access pattern differed from baseline, which may have contributed to some changes in pacing or visibility. Additionally, behavioural data were collected at the group level, which masks individual variation in feeding access, social interactions, and behavioural responses that may be particularly relevant in carcass-feeding contexts. Furthermore, in the absence of experimental-phase control data, conclusions reflect within-group changes under the specific management constraints of this facility. Nevertheless, the study provides a detailed account of how a carcass-based feast–fast schedule shapes 24-hour behaviour across a full feeding cycle.

Future studies would benefit from incorporating physiological measures, automated tracking, and replication across facilities with differing group compositions or enclosure designs. Varying cycle length or carcass type may further clarify how schedule structure affects activity, rest, and anticipatory patterns (Plowman, 2003; Hoy et al., 2010; Miller et al., 2020). Because the present analyses focused on behavioural expression rather than nutritional state, future work would benefit from incorporating direct measures of intake, chewing or manipulation time, and physiological markers related to nutritional balance and satiety to better evaluate how carcass-based feeding affects both feeding

mechanics and metabolic outcomes. As interest grows in evaluating feeding regimes over multi-day timescales, long-term 24-hour monitoring will be essential for capturing the full behavioural consequences of carcass-based feeding cycles.

5. Conclusion

This study examined behavioural responses to a whole-carcass feeding schedule in a small group of zoo-housed African lions implemented within a structured feast–fast cycle, using continuous 24-hour observations across three months. Carcass provision was associated with prolonged feeding and manipulation behaviours, followed by reduced locomotion and increased resting across subsequent fasting days. Pacing increased across months but showed little variation within each nine-day cycle, and standing exhibited only minor changes toward the end of fasting, patterns consistent with anticipatory responses to predictable management events rather than sustained arousal. Together, these findings demonstrate that feeding schedule structure can organise behaviour across both circadian and multi-day timescales, with effects extending beyond the day of carcass provision itself. Continuous 24-hour monitoring proved critical for capturing these temporal patterns. Although behavioural change alone cannot be used to infer welfare outcomes, the present results illustrate how whole carcass feeding regimes influence activity, rest, and anticipation, and underscore the importance of considering temporal structure when evaluating feeding practices in captive carnivores under comparable management conditions.

CRediT authorship contribution statement

Eduardo J. Fernandez: Writing – review & editing, Writing – original draft, Visualization, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Whittaker Alexandra:** Conceptualization, Supervision, Writing – original draft, Writing – review & editing. **Hryhorenko Lesia Marie:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Florence Demoulin:** Methodology. **Todd J. McWhorter:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Formal analysis, Data curation, Conceptualization. **Jon Allon:** Methodology. **Rachel Hemming:** Methodology. **Justine K. Partoon:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix 1. Interpretation of "Out of Sight" observations and visibility effects

"Out of sight" was recorded when lions were present in areas of the enclosure not visible to the cameras due to enclosure layout and camera placement. This category therefore reflects camera visibility rather than a behavioural state. Treating "out of sight" as a behaviour would misrepresent it as an activity, which it is not. Accordingly, variation in "out of sight" indicates periods when individuals were beyond the cameras' visual range rather than changes in motivation or engagement.

Figure A1 shows the proportion of scans coded as "out of sight" across the 24-hour cycle during baseline and the carcass-feeding phase. Periods of reduced visibility occurred primarily at night and corresponded to times when lions were housed in the larger on-exhibit enclosure. During daylight hours, visibility remained high across both phases, indicating that reduced visibility was structured by enclosure allocation rather than occurring randomly.

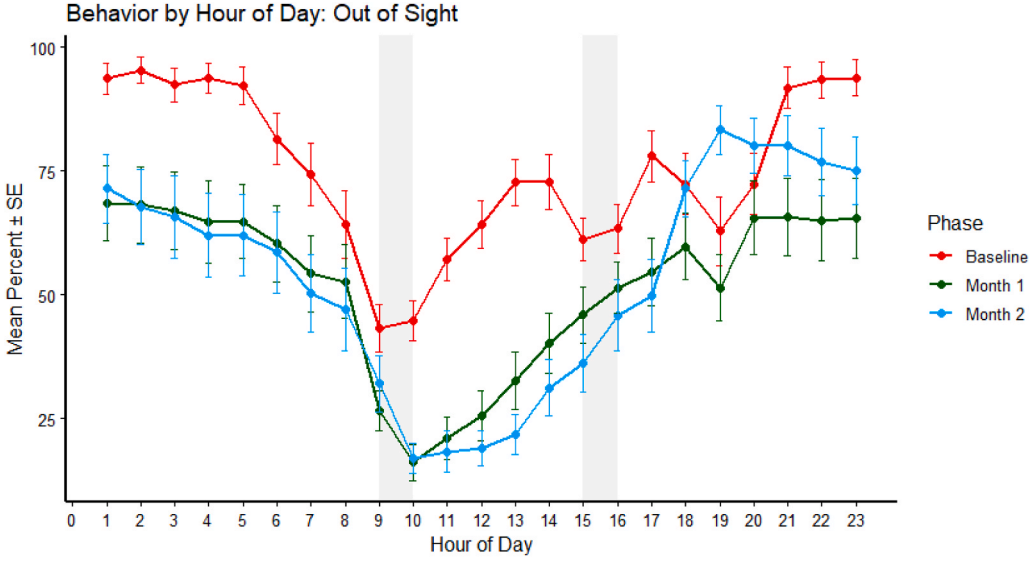

Figure A1. Proportion of scans coded as "out of sight" by hour of day across baseline and carcass-feeding phases

Visibility varied primarily by time of day rather than by position within the nine-day feeding cycle and did not increase systematically across fasting days. Periods of reduced visibility coincided with routine husbandry events, including scheduled shifting between enclosures, which are indicated by shaded regions in Figure A2.

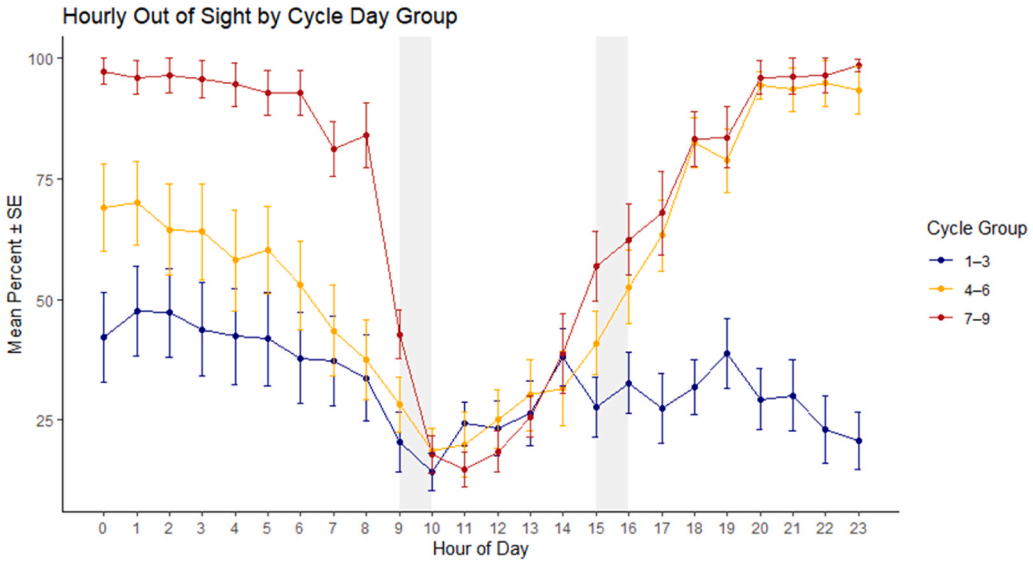

Figure A2. Hourly proportion of scans coded as "out of sight" across cycle day groupings (Days 1–3, 4–6, 7–9). Shaded regions denote typical periods of keeper shifting the lions between enclosures

To further evaluate whether reduced visibility influenced interpretation of key behaviours, the relationship between "out of sight" and pacing was examined using a linear model. There was no significant association between the proportion of scans coded as "out of sight" and pacing behaviour ($p = 0.136$, $R^2 = 0.028$), indicating that variation in visibility did not predict variation in pacing.

Together, these supplementary analyses demonstrate that "out of sight" primarily reflects enclosure allocation and camera coverage rather than unobserved behavioural activity. Inclusion of 24-hour data therefore preserves biologically relevant nocturnal feeding and post-feeding rest while allowing visibility constraints to be quantified and interpreted explicitly. Excluding night-time data would remove key components of the feeding cycle without materially improving behavioural inference.

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