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Positive Reinforcement Training Improves Behaviour and Welfare of Captive Indian Leopards (*Panthera pardus fusca*)

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ABSTRACT
Rescued animals, including leopards, often experience stress from routine husbandry practices such as feeding, movement, and regrouping. Positive Reinforcement Training (PRT) has emerged as a valuable tool for reducing stress and enhancing the welfare of captive animals. This study investigated behavioral changes in rescued leopards during structured PRT. Using continuous focal animal sampling, data on individual and social behaviors were collected during five-minute sessions conducted three times weekly over a period of 12–16 weeks. Twelve leopards were observed across five phases: Baseline, Pre-Training, During Training, Post-Training, and Trained. Statistical analysis using the Kruskal-Wallis test revealed significant behavioral changes across phases. Leopards required an average of 2.1 sessions (SD ± 4.43 days, N = 29 observations) to retrieve rewards consistently. Structured training led to significant reductions in undesirable behaviors, including aggression ($H(2) = 27.32$, $p < 0.0001$) and stereotypical pacing ($H(2) = 88.32$, $p < 0.0001$), while engagement behaviors such as locomotion and exploration increased. Affiliative interactions with caregivers also rose, indicating stronger bonds. A decline in out-of-sight behavior showed improved focus, while increased alertness and maintenance behaviors suggested enhanced cognitive flexibility. Overall, PRT fosters positive behavioral changes, improves emotional well-being, and strengthens human-animal bonds.

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KEYWORDS
Positive reinforcement training; stereotypic behavior; husbandry; pacing

Introduction

Modern zoos and rescue centers are built on a foundation of scientific knowledge, best husbandry practices, and ethical principles (Brando & Norman, 2023). Effective animal care prioritizes well-being, recognizing that positive welfare is an experience, not a gift from humans. When captive environments fail to meet species-specific needs, they induce stress, or "alarm reactions," which can harm both physical and psychological health, leading to illness or stereotypic behaviors (Schapiro et al., 2003).

This paper examines the role of these principles in shaping animal welfare and care in contemporary zoological settings. Animals are dependent on humans for their daily care and needs in captivity (Brando & Norman, 2023). Human-animal interactions may vary with their nature and can be positive or negative under certain circumstances (Collins et al., 2023). Animal caregivers and animals get more opportunities to become familiar with each other during routine husbandry practices such as feeding, cleaning, training, enrichment, and social interaction. These husbandry practices have some positively reinforced values for animals (Laule et al., 2016). Captive animals can become friendlier with caregivers than veterinarians (Carroll et al., 2022; Herron & Shreyer, 2014).

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The predictable and unscheduled events of husbandry practices influence animal behavior (Bassett & Buchanan-Smith, 2007; McDougall et al., 2006) toward the staff (Mellor et al., 2020). Animals can recognize and react differently to familiar and unfamiliar individuals (Williams et al., 2023). Interaction with an unfamiliar individual or event may lead to an abnormal behavior pattern among animals. Stereotypes in captive animals are tiresome acts, rigidly consistent behavior with no apparent goal or purpose (Lyons et al., 1997).

The use of operant condition-positive training to increase voluntary husbandry care is a major behavioral welfare advantage in zoos and aquariums since 1944 (Bennett 2023). Positive reinforcement Training (PRT) is a reward-based approach to behavior psychology to make veterinary and husbandry procedures easier and safer for animals and their caregivers (Otaki et al., 2015). PRT has been demonstrated to have positive impacts in reducing stereotypic behaviors in carnivores and can strikingly affect the quality of animal life (Shyne & Block, 2010; Weibel et al., 2021). PRT acts as an animal care and management tool that can help you to work closely with your animals, improve day-to-day husbandry practices and management practices, coordination with animals and staff, and help to learn animal's needs (Fazio et al., 2020). PRT may provide the participating animal with positive social interaction, cognitive stimulation, and choice (Weibel et al., 2021). PRT enhances the animals' control and predictability, offering potential welfare benefits (Bassett & Buchanan-Smith, 2007). Implementing PRT in animal care and management can dramatically affect the quality of animal's life (Chapman & Dobbs, 2023). A comprehensive approach is essential, and zoos or rescue centers should aim to ensure the highest standards of welfare for the animals in their care. Like the majority of felines, the Leopard *Panthera pardus* is solitary, whereas in captivity they are sometimes successfully maintained as pairs, trios, or larger groups (De Rouck et al., 2005; Pastorino et al., 2021). The captive big cats have a greater capacity for social interaction (Vaz et al., 2022) with conspecifics, parents or siblings, and caregivers. These interactions are quite complex, and past research has contributed toward understanding their influence on the personality and stress physiology of big cats (Narayan et al., 2017). The training program at Center focused on reducing aggressive and stereotypic behavior of grouped Indian Leopards in a captive condition. Our study focused on PRT and building the animal and caregiver relationship. First, we aimed to evaluate the effect of PRT training on Leopard's behavior in the presence of a caregiver and trainer. To achieve this aim, we compared the behavior of the Leopards before the beginning of the training program (baseline phase), during the training phases, and, after completing the training. In addition, we also predicted that PRT would help reduce aggression and agonistic behavior toward the keeper and conversely increase affiliative or participatory behavior.

If the PRT training had a positive influence on the welfare of the Leopards, we would predict a qualitative and quantitative rise in the performance of species-typical behavior (Mellor et al., 2020). On the other hand, if PRT training was to impact pessimistically on the welfare of the Leopards, modifications in the Leopard behavioral repertoire would be expected; in particular, abnormal and stress-related behavior, as well as aggressive behavior, would be displayed more than baseline phase.

Methods

2.1 *Subjects and Housing*

Twelve adult Indian Leopards (*Panthera pardus fusca*) were involved in this study since they were from a Human-Leopard conflict background and of a stereotypic nature. There were eight males and four females of mix age groups (2.5–13 yrs.; Table 1) rescued from different parts of the India and received by center during the year 2020–2021. Animals were housed either in isolation, in pairs, or trios. For individual details (regarding sex ratio, age, grouping, and housing) refer to Table no.1. The open-air outdoor naturalistic habitat included trees, grasses, logs, caves, ponds, bush cover, bamboo cover, and one training area adjacent to the chain-link. The study was structured into five phases: Baseline phase, Pre-training, Training, Post-training, and Trained. The Baseline phase was

Table 1. The details about group housing, area available, sex, and age of subjects i.e., Indian leopards (*Panthera pardus fusca*) housed at center. The table reports the sex (F = female; *M* = male) and the age (years at the time of data collection) as well as the area of housing (night house and paddock area in square meters).

Sr No	Name	Group ID	Sex	Age	Night house	Paddock
1	Jai	1	M	6.5	78	547
2	Veeru	1	M	5.5	78	547
3	Atal	1	M	5.3	78	547
4	Ela	2	F	2.5	40	143
5	Bagheera	2	M	3	40	143
6	Rock	3	M	13	78	547
7	Van	3	M	10	78	547
8	Bala	3	M	12.5	78	547
9	Nytiri	4	F	5	40	547
10	Savitri	4	F	4.5	40	547
11	Ram	5	M	11	40	143
12	Sita	6	F	9	40	143

conducted before any interaction or training took place. The Pre-training, Training, and Post-training phases occurred during the training progression, while the Trained phase began once animals reliably exhibited the desired behavior. Data were collected during each of these phases to evaluate behavioral changes.

Study design

Behavioural data collection

In both the baseline and training phases continuous focal animal sampling was used (Altmann, 1974) to collect data on the behavior of the leopards in the social context. In the Baseline phase, five minutes sessions per leopard were run and data was collected. For each subject, three sessions per week were carried out in the evening between 4:00 pm and 6:00 pm, over a 12–16-week time. In both the baseline and training phases, data on individual (locomotion, exploratory, alert, sleeping, maintenance, scent marking, feeding, stereotypic, and inactive behaviors) and social (agonistic, aggressive, grooming, playing, social contact, social sleeping, affiliative) behaviors were collected in seconds for five-minute observation period (Table 2). Time spent out of sight was also recorded, as hiding is considered a natural behavior in response to stress or environmental threats (Collins et al., 2023). Observations during the Pre-training phase were collected immediately before each training session, while Post-training observations were collected immediately after each session on the same day. During training observations were recorded throughout the training process. Trained phase data were collected once animals consistently demonstrated the trained behavior.

Table 2. Ethogram used for Indian leopard (*Panthera pardus fusca*) during the baseline and training phases.

Behaviour	Description
Out of Sight	Hiding, not visible
Ignorance	Ignore the presence of caregiver and staff, avoid, flee
Inactive	Sitting, sleeping, lying, standing, stretching
Aggression	Attack, bare teeth, bite, charge, chase, crouch, fight, ground slap, kill bite, rear, snarl, tail slap, tail swish twitch
Agonistic	Threaten, arch back, hiss, snap bite, social stare, tail over, displace, tail under, piloerection
Locomotion	Walking, Trotting, Stalk, Running, Jumping, Climb, Approach
Exploratory	Sniff, Lick, Flehmen, Ears erect, Ears forward, Dig, Paw, Rear, Chew, Watch
Patrolling	Area survey including scent marking
Pacing	Stereotypic constant aimless movements
Alert	Ears side, tail tip motion, vocalization, investigation
Maintenance	Defecate, groom, clawing, urinate, vomiting, scraping, solitary roll
Affiliative	Anogenital sniff, Play, follow, play, roll on back, sniff nose, lick, huddling, gurgle
Feeding	Carry, Eat, Drink

Creating training conditions

PRT was conducted from outside the paddock. As per standard safety protocols for large carnivores (like Lions, Tigers, Leopards, Bears, Hyenas, etc.), direct contact was avoided, with at least one barrier in place between the animals and caregivers. A wooden platform (minimum 50 cm wide, 50 cm high, and 300 cm long) was fitted next to the chain-link fence to allow leopards to settle near the barrier. This platform was used to provide food enrichment and to habituate the animals to the training area during the initial fifteen days habituation period. This habituation occurred before the start of the Pre-training phase, allowing leopards to get used to the training setup.

Food enrichments were given continuously to all individuals inside respective paddocks to create a healthy atmosphere and psychology; this approach helped reduce competition and stress, thereby supporting a cooperative environment for learning. This strategy help build the confidence in animals for conditioning. Each Leopard was given a unique name based on its nature and rosettes on its face and flank. Trainers and caregivers were asked to call an individual by their names while doing every activity like feeding or while taking observations. During all baseline data collection and training sessions, both a keeper and a trainer were present. Meat rewards used during training were weighed and formed part of the animals' diet and sometimes with extra 50–100 gm. The reward was a piece of boneless chicken neck or liver, which the leopard found pleasant. Each piece of meat was approximately 2 cm by 2 cm.

During habituation, the sliding doors and drop gates of the night houses remained open, allowing leopards to voluntarily access the paddock and collect rewards placed on the platform.

Whistle conditioning - building a bond

A combination of classical and operant conditioning was used to train these Leopards (Shyne & Block, 2010). Before initiating the formal Training phase, the first step involved basic whistle conditioning. A high-quality, stainless steel whistle with adjustable frequency was used. Over ten days, the whistle sound (conditioned stimulus) was repeatedly paired with a food reward (1–1.5-inch boneless chicken, liver pieces – unconditioned stimulus). Initially, the trainer whistled every 30–60 seconds in front of the Leopard. Subsequently, using 8-inch-long stainless-steel tongs (for safety reasons), a piece of chicken reward (positive reinforcement) was given immediately after the "whistle" sound. This attempt was repeated 2 to 5 times per session, twice a day, for a minimum of 15 days. After each successful response, the session was finished with a single voice reward ("Very good" or "Shabbas"), and at the last attempt, the trainer would give 2–3 extra pieces as a final reward, signal the end of the session by waving hands, in front of the Leopard, and immediately exit the training area. This schedule was followed continuously for a minimum of 15 days, based on the individual animal's response. Once animals were classically conditioned to associate the whistle "beep" sound with the food reward, and recognized it was followed by a reward, whistling was ultimately used as a bridging stimulus for positive reinforcement training (Otaki et al., 2015). During training session, food rewards were offered using variable intervals to stay unpredictable (Callealta et al., 2020; Pomerantz and Terkel, 2009). This helps to keep the animal's attention high.

Positive Reinforcement Training (PRT)

All leopards were provided unrestricted access to both the indoor and outdoor areas of their enclosures prior to the onset of training, ensuring that enclosure use remained voluntary and uninterrupted despite ongoing routine management activities within the captive environment. Following this period, individuals were required to voluntarily approach the designated training area to receive rewards from the trainer. The indoor and outdoor areas were connected by a sliding steel gate with a transparent acrylic sheet, allowing for unrestricted movement. Leopards could observe conspecifics and staff, enabling them to make informed decisions about when to enter the training area. If no leopard entered within five minutes, the session was concluded.

In the second phase, target training involved a 50 cm stainless steel rod with a colored tennis ball (Figure 1). Leopards were encouraged to touch the target, and upon contact, a whistle was sounded,

Figure 1. Trainer showing leopard conditioning to settle down using PRT in habitat.

followed by a food reward. As training progressed, the target was moved to different locations to encourage further engagement. If undesirable behaviors (e.g., aggression or avoidance) occurred, the trainer paused and resumed once the leopard had calmed.

To minimize stress, training sessions were kept under five minutes per leopard. Sessions were conducted daily for 9–12 weeks, concluding when a leopard retrieved the reward consecutively for 4–5 sessions. Following target training, leopards underwent desensitization training, though this was not part of the current study.

Behavioral data, including feeding time, social interactions, and signs of stress (e.g., aggression or stereotypical pacing), were recorded during each session. These data were analyzed to determine whether the leopards were able to remain calm and voluntarily participate in husbandry, veterinary care, and research activities.

Data analysis

The analysis aimed to assess the effects of different training conditions on animal behaviors, particularly focusing on aggression and pacing. All statistical analyses were performed using R statistical software (v4.4.1; R Core Team 2024) with a significance level of $p \leq 0.05$. Plots were made using Elegant Graphics for Data Analysis (H. Wickham. Ggplot2; Springer-Verlag New York, 2016). Initially, we planned to use a mixed-effects model with individual as a random effect and training conditions as a fixed effect; however, due to the relatively small sample size and imbalances among individuals, and following a statistician's recommendation, we opted for a less complex approach. Since the data were not normally distributed, we applied the non-parametric Kruskal-Wallis test to compare behaviors across Leopards and training phases (Baseline, Pre-Training, During Training, Post-Training, and Trained). Post hoc comparisons were performed using Dunn's test with Bonferroni correction to identify specific group differences.

Furthermore, the relationship between training progress and behavior was evaluated using line graphs constructed with ggplot2. A Mann-Whitney-Wilcoxon rank-sum test was used to assess whether the level of aggression and affiliation differed among the sex of the subjects during the training sessions.

For descriptive statistics related to session and engagement data, Mean ± standard deviation (SD) was calculated. For behavioral data, which were non-normally distributed, we have reported the values as Median ± interquartile range (IQR) in the corresponding table. Statistical significance was set at $p \leq 0.05$.

Results

Leopard response within the training session

On average, Leopards required 2.1 sessions (SD ±4.43 sessions, $N = 29$ observations) to retrieve the reward over four consecutive days during DT phase. Initially, they interacted minimally with trainers, typically ignoring them for an average of 3.3 days (SD ±4.46 days). During these early sessions, Leopards generally disregarded trainers for brief periods, with observed durations ranging from 5 seconds to a maximum of 178 seconds (43.3 sec. ±28.40 sec.) during the training sessions. In the mid-training phase, all leopards began engaging more consistently, indicating acclimatization to the program. By this stage, their engagement time peaked, reaching a maximum of 60 seconds, with an average engagement duration of 21.8 seconds (SD ±11.52 sec.).

Effect of the training phases on the leopard behaviour

The Kruskal-Wallis test revealed significant differences across training phases for several behaviors, indicating clear changes in behavioral patterns as training progressed (Table 3). Significant results were further explored using Dunn's post hoc tests to identify specific pairwise differences (Table 4). During the study, stereotypic pacing and species-specific behavior were observed in the leopards.

Indicators of human-leopard relationship

(Includes: out of sight, ignorance, aggression, agonistic, affiliation). Out of Sight and Ignorance behavior

Table 3. Behaviors observed in the baseline and training period. The table reports the median duration in seconds (M) and the interquartile range (IQR) for each behavioral category in both the baseline and the training period, along with the χ^2 -value, and the P-value from the Kruskal-Wallis test for the comparison between the five conditions. *p* value indicates behavioral categories for which a significant difference between the training conditions was found (Kruskal-Wallis test: p < 0.001).

Behaviour	B[a]	PrT[b]	DT[b]	PoT[b]	T[c]	χ^2	p
OoS	0 [58]	13 [47.75]	0 [0]	0 [21]	0 [0]	52.02	0.0001
Ina	0 [91.75]	51.5 [89]	41 [87.5]	68.5 [105.75]	89.5 [65.25]	17.11	0.0018
Ago	0 [19.5]	0 [11]	0 [11]	0 [5]	0 [0]	33.335	1.02e-6
Agg	0 [11]	0 [7.25]	0 [5]	0 [0]	0 [0]	27.32	0.0001
Loco	15 [76.75]	87 [54.5]	73 [55.5]	79 [68.5]	86 [43.25]	64.573	0.001
Expl	0 [0]	23.5 [42]	19.5 [32]	22 [51.25]	30.5 [60.25]	100.87	0.001
Ptrl	0 [0]	0 [34.25]	0 [0]	0 [0]	0 [23.25]	37.722	0.001
Pacg	0 [183.75]	0 [0]	0 [0]	0 [0]	0 [0]	88.316	2.2e-16
Alt	0 [11]	30.5 [27.25]	43 [38.5]	32 [29.5]	34.3 [29.75]	166.07	2.2e-16
Mant	0 [0]	0 [0]	17.5 [27]	9.5 [22]	0 [21]	109.61	2.2e-16
Igr	0 [22]	0 [11]	0 [15.75]	0 [17.75]	0 [0]	39.125	0.001
Affiliative	0 [0]	0 [1.25]	0 [12.25]	0 [0]	0 [16.25]	39.125	0.001

" >Behv (Behaviour codes), OoS (Out of Sight), Ina (Inactive), Igr (Ignorance), Agg (Aggression), Ago (Agonistic), Loco (Locomotion), Expl (Exploratory), Ptrl (Patrolling), Pacg (Pacing), Alt (Alert), Mant (Maintenance), Aff (Affiliative). Training Phases: (B) Baseline, (PrT) Pre-Training, (DT) During-Training, (PoT) Post-Training, and (T) Trained. [a]$n = 175$. [b]$n = 100$. [c]$n = 84$.

Table 4. Post hoc pairwise comparison of group differences using Dunn's test with bonferroni correction for different behaviors in various training phases.

Behv	B X PrT	B X DT	B X PoT	B XT	DT X PrT	DT X PoT	DT X T	PoT X PrT	PoT X T	PrT X T
OoS	−1.60	−4.59[c]	1.41	−4.42[c]	−5.69[c]	−2.92[b]	0.06	−2.77[b]	2.86[b]	5.50[c]
Igr	0.53	0.94	−0.52	3.16[c]	1.35	0.39	3.76[c]	0.96	3.39[b]	2.47[a]
Ago	0.31	0.13	2.79[b]	4.82[c]	0.40	2.68[b]	4.59[c]	−2.28[a]	2.02	4.20[c]
Agg	0.50	−0.97	2.79[b]	4.69[c]	−0.44	1.68	3.50[c]	−2.11	1.89	3.91[c]
Loco	−6.36[c]	4.98[c]	−5.74[c]	−6.33[c]	−1.27	−0.69	−1.49	−0.57	−0.82	−0.28
Expl	−7.00[c]	5.72[c]	−7.30[c]	−8.62[c]	−1.18	−1.45	−2.96[b]	0.27	−1.57	−1.84
Ptrl	−4.91[c]	−0.29	−2.19[a]	−3.62[c]	−4.79[c]	−2.29[a]	−3.62[c]	−2.50[a]	−1.44	0.96
Alt	−7.79[c]	11.57[c]	−8.61[c]	−8.63[c]	3.47[c]	2.72[b]	2.16[a]	0.75	−0.44	−1.15
Mant	−0.03	8.76[c]	−5.94[c]	−4.50[c]	8.04[c]	2.60[b]	3.54[c]	5.45[c]	1.05	−4.15[c]
Aff	−1.71	4.91[c]	−0.67	−4.66[c]	2.94[b]	3.90[c]	−0.001	−0.96	−3.73[c]	−2.81[b]

" >Training phases: B (Baseline ($n = 175$)), PrT (Pre-training ($n = 100$)), DT (During Training ($n = 100$)), PoT (Post-training ($n = 100$)), T (Trained ($n = 84$)). Behv (Behaviour codes), OoS (Out of Sight), Igr (Ignorance), Agg (Aggression), Ago (Agonistic), Loco (Locomotion), Expl (Exploratory), Ptrl (Patrolling), Alt (Alert), Mant (Maintenance), Aff (Affiliative). Z-statistics are reported with Bonferroni-adjusted p-values: $p < 0.05$ [a], $p < 0.01$ [b], $p < 0.001$ [c].

The results of the analysis show how the transitions between different training phases B, PrT, DT, PoT, and T influence Out of Sight behavior. A significant reduction in Out of Sight behavior is observed when comparing the B phase to DT and T phase as indicated by the negative Z-scores (Table 4). This suggests that the active training and post-training phases are highly effective in reducing Out of Sight behavior. Significant findings indicate that the DT phase plays a crucial role in reducing Out of Sight behavior, particularly when paired with the PrT and PoT phases.

The ignorance behavior was evident during the B period, where leopards tended to show ignorance behavior toward the trainers. However, this behavior significantly decreased as training progressed.

Aggression behavior

Aggression behavior showed a clear decreasing trend across the training phases. Median aggression levels (with IQR) were highest in the B phase, followed by PrT, DT, and PoT, with the lowest levels observed in the T phase (Table 3, Figure 2).

These trends are supported by significant differences in pairwise comparisons. Specifically, aggression was significantly lower in T phase compared to B and PrT phases (Table 4). Additionally, a significant decrease was observed between PoT and Prt, and between B and PoT. However, comparisons between B and PrT, B and DT and Dt and PrT did not yield significant difference.

Notably, aggression behavior was significantly lower in the T phase compared to the B and PrT phases. There was also a decreased in aggression from PoT to T phase. Comparisons between DT and B phases showed marginal significance. Furthermore, a notable reduction in aggression behavior was observed in the T phase compared to both the DT and PrT phases (see Table 4).

The Mann-Whitney-Wilcoxon rank-sum test revealed no significant difference in aggression between male and female subjects ($W = 30742$, $p = 0.9191$). There was no significant difference in aggression during the B phase ($H = 3.56$, $p = 0.059$) or the T phase ($H = 0.556$, $p = 0.45$) across the animal groups. A marginal trend was observed between the isolated (Group 1) and trio (Group 3) animals ($z = -1.89$, $p = 0.059$), indicating a potential but non-significant difference in aggression between these two groups.

Agonistic Behaviour

The agonistic behaviors were more prominent during the B phase and decreased progressively across the training phases, with the lowest levels observed in the T phase (Table 3). This overall reduction in agonistic behavior was statistically significant ($\chi^2 = 33.335$, $p = 1.02e{-6}$; Table 4). Pairwise comparisons showed significantly lower agonistic behavior in the T phase compared to the B, PrT, and DT phases. Significant reductions were also found between B and PoT, DT and PoT,

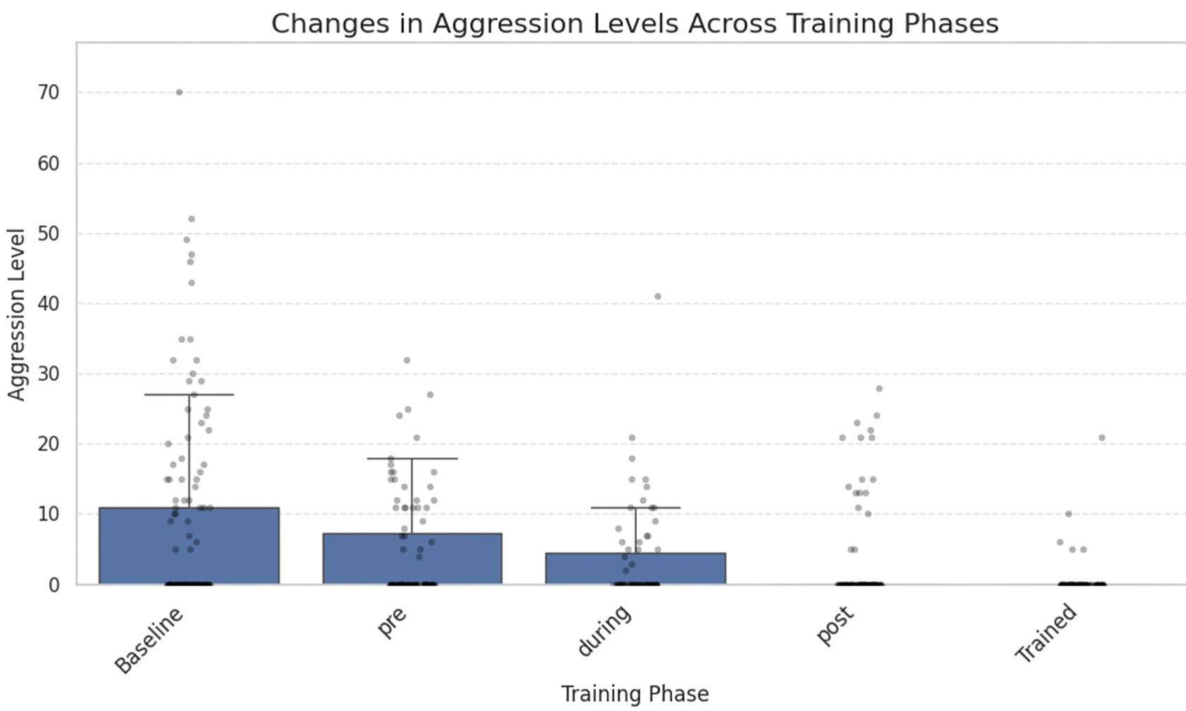

Figure 2. Training-induced reduction in aggressive behavior.

Box plots depict aggression level (in seconds) distributions across phases (Baseline, Pre-training, During Training, Post-training, Trained), ordered by descending median. Each plot shows the median (line), IQR (box: 25th –75th percentiles), and whiskers (≤1.5×IQR). Black dots represent individual observations.

and PoT and PrT. In contrast, comparisons between B and PrT, B and DT, DT and PrT, and PoT and T were not statistically significant. These results demonstrate a phase-dependent decline in agonistic behavior during the training process.

Affiliative Behaviour

The Kruskal-Wallis test revealed notable variation in affiliative behavior across training conditions. Affiliative behavior was significantly more frequent during the DT phase compared to the B, PoT, and PrT phase. Additionally, affiliative behavior was considerably lower in the B and PoT phases compared to the T phase (Table 4). The Mann-Whitney-Wilcoxon rank-sum test showed a significant difference between sexes ($W = 34509$, $p = 0.0024$). No significant differences in baseline affiliation levels were found across animal groups ($H = 2.87$, $p = 0.09$). Similarly, there were no significant differences in trained affiliation levels ($H = 0.176$, $p = 0.67$), and Dunn's test confirmed the absence of significant pairwise differences ($Z = -0.420$, $p = 0.67$).

Indicators of leopard welfare

(Includes: Locomotion, Exploratory, Patrolling, Pacing, Alert, Maintenance).

Locomotion, Exploratory, and Patrolling Behaviour

There are significant differences in locomotion between several conditions. Notably, animals exhibited increased locomotion in DT compared to when they were in the B phase and decreased locomotion once in the T phase compared to the B phase. Additionally, locomotion was significantly lower in the T phase compared to those that were in the B phase. Other comparisons, such as DT vs. PoT and DT vs. PrT, were not significant (Table 4). Animals engaged significantly more in exploratory behavior during DT compared to B phase. Furthermore, B phase showed significantly less explorative behavior than T phase. Other notable comparisons included significant differences between B and PoT and B and PrT phases. Comparisons such as DT vs. PrT and DT vs. T also showed significant differences (Table 4). Dunn's test results showed significant decreases in patrolling behavior in DT compared to PrT, B phase and PoT. In the B phase, individuals also exhibited reduced patrolling behavior compared to the T phase. Other comparisons were not significant, like the DT vs. B phase and the PrT vs. T phase (Table 4).

Pacing Behaviour

Stereotypic pacing behavior, observed in a subset of individuals ($n = 8$ leopards, Figure 3), decreased with training progression. Pacing behavior was significantly more prominent during the B phase when no training was conducted compared to all subsequent phases where training was either in progress (DT phase) or completed (T phase) (see Table 3). However, no significant differences were found between the phases when training was ongoing (DT and PoT), nor between these phases and after finishing training (T phase).

Alert and Maintenance Behaviours

There was a notable difference in alert behavior across the training conditions, with leopards displaying more alert behavior during the DT and T phases compared to the B phase. Additionally, maintenance behavior, which was absent during the B phase, became more apparent as the animals progressed through the training phases. Maintenance behavior during the DT phase was significantly higher than in the B and PrT phases. Furthermore, maintenance behavior during the PoT phase was significantly greater than in the B phase.

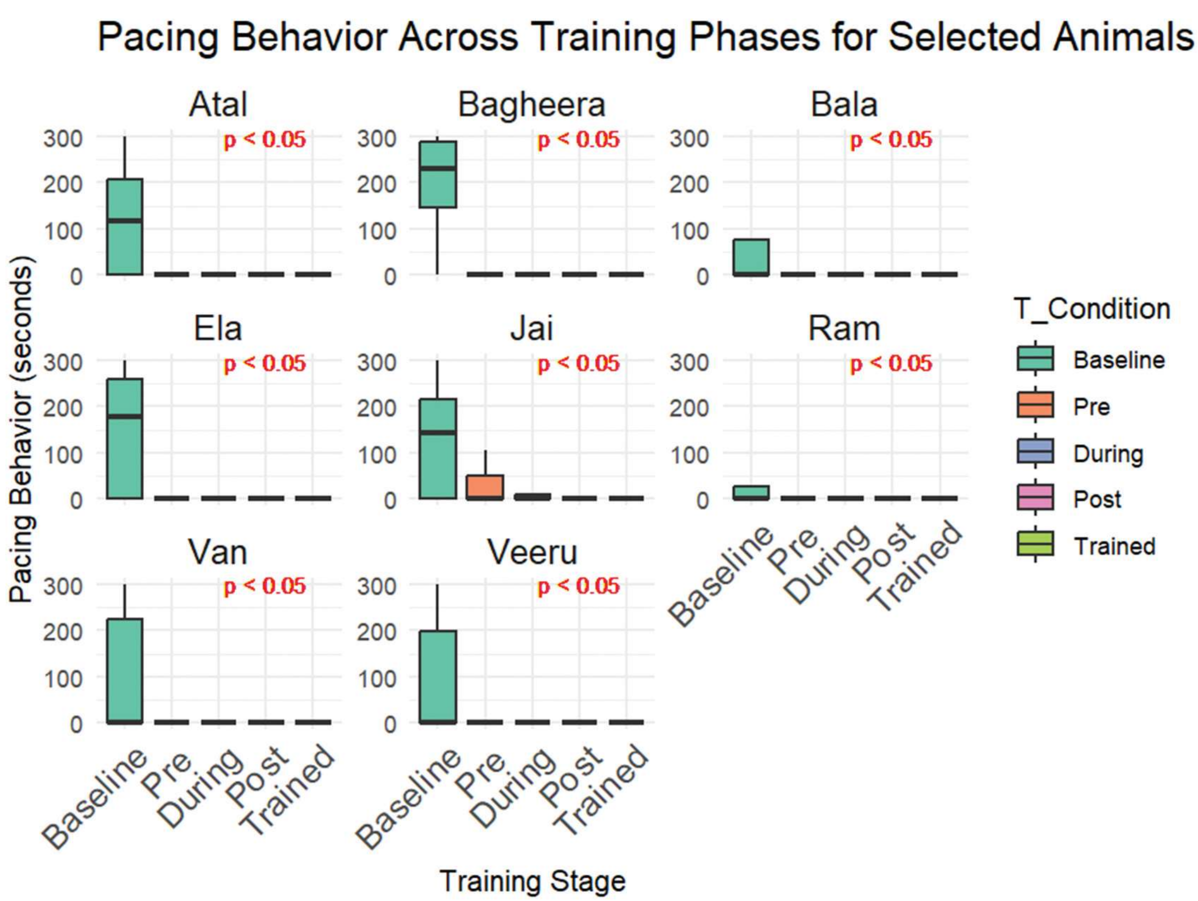

Figure 3. Pacing behavior across the training phases for selected animals.

Discussion

The primary aim of this study was to evaluate the impact of PRT on the behavior of Indian Leopards in a captive setting, focusing on two main hypotheses: (1) that PRT improves the human-leopard relationship by reducing aggression and avoidance behaviors while increasing affiliative behavior, and (2) that PRT enhances leopard welfare by reducing stress-related behaviors and promoting more natural, species-typical activity. To align with these objectives, we have discussed the findings in two thematic areas: Indicators of Human-Leopard Relationship and Indicators of Leopard Welfare. Our findings support both hypotheses, indicating that structured training can be a valuable tool for improving the behavioral and emotional well-being of captive leopards.

Indicators of human-leopard relationship

Out of sight and ignorance behaviour

Out of sight behavior, which includes distractions or disengagement from the training task, was significantly reduced during the training phases. These results demonstrate that structured training programs can help improve task engagement and reduce distractibility (Hintze & Yee, 2023). The DT phase was crucial in reducing out of sight behavior, likely due to the structured nature of active training that encourages consistent attention to the task at hand. The observed reduction throughout the active training phases reflects a more focused state for task performance in the leopards (Lomb et al., 2021). Additionally, the transition from PrT to PoT, and from PoT to T, also contributed to a decrease in out of sight behavior, suggesting that post-training acclimatization and reinforcement were effective in maintaining attention and reducing distractions.

The decrease in ignorance behavior as training progressed suggests that positive reinforcement facilitated increased engagement between the leopards and their trainers. This decline in avoidance behaviors during structured training and positive interactions can strengthen human-animal bonds and reduce stress-related responses (Heidenreich, 2007), as similarly demonstrated in training programs with other captive carnivores, reinforcing the generalizability of these effects.

Aggression and agonistic behaviour

The significant decrease in aggression behavior aligns with the notion that training not only improves task performance but also helps regulate emotional responses, such as aggression (Riemer et al., 2021). The significant reduction in aggression from PoT to T can be attributed to the positive reinforcement during DT and PoT phases, which likely increased the leopards' comfort with the training environment. Previous studies have shown that positive human-animal interactions in PRT can reduce both inter- and intra-specific aggression outside the training context, supporting the idea that PRT may enhance coexistence between animals and caregivers (Brando & Norman, 2023). Watters (2014) also discusses how formal training can lead to reduced stress and negative emotional states by empowering animals, which aligns with our observed aggression decreases. This lack of difference may suggest that initial exposure to trainers alone is insufficient to reduce aggression, consistent with Leeds et al. (2016), who noted that contextual enrichment and trainer familiarity are critical to behavioral changes. This aligns with Riemer et al. (2021), who documented that continued reinforcement improves coping strategies and diminishes aggressive tendencies over time.

The higher occurrence of agonistic behaviors during phase B suggests that leopards may have experienced higher levels of stress or frustration due to a lack of structured engagement. However, as training progressed, particularly during the PoT and T phases, these behaviors decreased, indicating that positive reinforcement training possibly alleviated stress and fostered more cooperative and relaxed interactions (Brando & Norman, 2023).

Affiliative behaviour

The increased affiliative behavior during the DT phase, compared to other phases, indicates that the leopards formed stronger positive associations with the trainers as they became more accustomed to the training process. This was likely due to the positive reinforcement employed during training, which is known to foster positive emotional responses and strengthen human-animal bonds (Brando & Norman, 2023). Moreover, the significantly lower affectionate behavior during the B and PoT phases compared to the T phase suggests that the leopards' relationship with trainers became more positive as they transitioned from pre-training to the final trained phase. Fernandez (2022) further supports this by emphasizing that training not only modifies interactions but expands behavioral repertoires in ways that enrich animal welfare.

Sex differences in aggression and affiliative behaviour

Interestingly, the Mann-Whitney-Wilcoxon rank-sum test revealed no significant sex differences in aggression behavior, but significant differences were found in affiliative behavior, with females exhibiting more affection toward trainers. This is consistent with other studies in which female animals have been shown to exhibit higher affiliative behaviors compared to males, potentially due to differing social dynamics or hormonal influences (Kemp et al., 2017; Spiezio et al., 2017).

Group differences in aggression and affiliative behaviour

There was no strong evidence of group differences in aggression or affiliation, as neither baseline nor trained aggression and affiliation reached statistical significance. While some trends, such as baseline aggression between isolated and trio animals, approached significance, they did not meet the $p < 0.05$ threshold, suggesting no clear differences under the experimental conditions. Housing conditions appeared to have minimal impact on these behaviors, although further research is needed to identify potential contributing factors.

Indicators of leopard welfare

Locomotion, exploratory and patrolling behaviour

Consistent with Puehringer-Sturmayr (2023) findings, the enriched and interactive environment during the DT phase led to increased locomotion, indicating that the engaging sessions encouraged more movement. Conversely, locomotion decreased once the leopards entered the T phase, which could reflect a shift from exploration to more task-oriented behavior as they became acclimatized to the training regimen. Additionally, exploratory behavior increased during DT compared to the B phase, indicating that the training environment encouraged the leopards to explore their surroundings more actively. This finding aligns with the concept of environmental enrichment in animal training, which promotes cognitive and behavioral flexibility by providing stimulating, dynamic environments that encourage natural behaviors, problem-solving, and adaptability (Young et al., 2020). Interestingly, exploratory behavior was more prominent in the T phase, suggesting that the training provided cognitive stimulation that enhanced exploration. Patrolling behavior was significantly lower during the B phase, suggesting reduced activity or engagement in the absence of training. A noticeable increase in patrolling was observed at the beginning of training (DT and PrT), indicating heightened alertness and responsiveness (Mason et al., 2007).

In particular, we observed a significant increase in patrolling behaviors during the training period compared to the baseline period, a finding that contrasts with previous research on PRT (Spiezio et al., 2017). Previous studies have typically reported general increase in activity levels as a consequence of animal training (Melfi, 2013). A possible explanation for the observed increase in patrolling could be the leopards' adaptation to the enriched training environment, which may have facilitated greater environmental engagement and alertness. The absence of significant differences between "DT" and later phases suggests that patrolling behavior stabilized as the leopards acclimatized to the training routine. This plateauing effect is consistent with findings by Melfi

(2013), who reported that animals reached behavioral equilibrium after an initial increase in activity following exposure to enrichment. Westlund (2014) asserts that formal training serves as enrichment by stimulating species-appropriate covert behaviors, such as those associated with foraging motivation, which could explain the increase in exploratory and patrolling behaviors observed during the training phases.

Pacing behaviour

The reduction in stereotypic pacing observed in the leopards aligns with previous studies suggesting that training and environmental enrichment can reduce stress-related behaviors in captive animals (Brando & Norman, 2023). This supports the findings of Brando and Norman (2023), who noted that the inclusion of choice and control elements – such as outdoor settings – can significantly improve welfare outcomes. In the B phase, where no training occurred, pacing was more prominent, indicating higher stress levels. However, during and after the training, pacing decreased significantly, suggesting that PRT in a structured environment helped alleviate stress (Rasmussen et al., 2020). Unlike traditional PRT, which is often conducted in enclosed spaces, the center implemented training in an outdoor habitat, allowing leopards to voluntarily engage with the process in a more natural setting. This approach likely contributed to the reduction in stereotypic behaviors, highlighting the importance of providing choice, mental stimulation, and environmental enrichment to improve the welfare of captive animals. Anderson et al. (2020) cautioned that anticipatory behaviors may reflect a state of "wanting" rather than positive emotion per se, emphasizing the need to interpret reductions in pacing with caution and within the broader context of animal motivation and welfare(Podturkin et al., 2022).

Alert and maintenance behaviours

The prominent occurrence of alert behavior in the DT and T phases suggests that the leopards developed greater cognitive and behavioral flexibility as they adapted to the training program (Mason et al., 2007). Similarly, maintenance behavior, which was not evident in the B phase, became more apparent in the DT and T phases. Maintenance behaviors likely reflect the leopards' increased attention to the task, which could involve observing and manipulating their environment in a more sustained manner (Spiezio et al., 2017). The significant increase in maintenance behavior during the DT phase suggests that the leopards began to develop a more focused approach to their training tasks as they progressed through the phases. This supports Westlund's (2014) hypothesis that formal training fosters animals' ability to adapt and respond flexibly to changing environments, thereby enhancing psychological well-being.

Conclusion

This study demonstrates that PRT has a significant positive impact on the behavioral and emotional welfare of captive Indian leopards. The results show that structured training not only reduces negative behaviors like aggression and stereotypic pacing but also fosters affiliative behaviors and species-typical activity. By enhancing task engagement and reducing avoidance behaviors, PRT supports emotional regulation and improves the overall well-being of the leopards.

Consistent improvements in behavior were observed as the leopards progressed through training, with reductions in stress-related behaviors – most notably, aggression and avoidance. Additionally, increased locomotion and exploration during training phases reflect the cognitive stimulation and behavioral engagement facilitated by PRT, which enhances behavioral flexibility and mental stimulation. These behavioral improvements – as supported by prior research (Westlund, 2014; Brando & Norman, 2023) – underscore the value of incorporating PRT into animal management protocols, offering both cognitive enrichment and enhanced human-animal interactions.

However, the study's limitations, such as its small sample size and short-term focus, highlight the need for expanded future investigation. Future studies should assess the long-term effects of PRT on welfare outcomes, including physiological indicators such as cortisol levels, and explore its influence on social dynamics in group-housed individuals.

This research contributes to the growing body of evidence supporting structured PRT as a practical and effective approach to improving the welfare of captive animals. Although PRT is widely used with other big cats, few studies have examined its application specifically in Indian leopards. This gap highlights the relevance of the present study, which aims to improve the welfare of rescued captive leopards by applying PRT. By fostering more adaptive behaviors, reducing stress, and promoting overall psychological well-being, this work provides valuable guidance for advancing best practices in captive wildlife care and training.

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References

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, *49*(3–4), 227–266. https://doi.org/10.1163/156853974X00534

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. https://doi.org/10.7120/09627286.29.3.231

Bassett, L., & Buchanan-Smith, H. M. (2007). Effects of predictability on the welfare of captive animals. *Applied Animal Behaviour Science*, *102*(3–4), 223–245. https://doi.org/10.1016/j.applanim.2006.05.029

Bennett, K. (2023). *A human-animal dialogue: Positive reinforcement training in zoos and aquariums*. *Student Theses 2015-Present. 148*. https://research.library.fordham.edu/environ_2015/148

Brando, S., & Norman, M. (2023). Handling and training of wild animals: Evidence and ethics-based approaches and best practices in the modern zoo. *Animals*, *13*(14), 2247. https://doi.org/10.3390/ani13142247

Callealta, I., Lueders, I., Luther-Binoir, I., & Ganswindt, A. (2020). Positive reinforcement conditioning as a tool for frequent minimally invasive blood and vaginal swab sampling in African lions (Panthera leo). Journal of Applied Animal Welfare Science, 23(4), 508-519. https://doi.org/10.1080/10888705.2019.1709066

Carroll, S. L., Sykes, B. W., & Mills, P. C. (2022). Moving toward fear-free husbandry and veterinary care for horses. *Animals*, *12*(21), 2907. https://doi.org/10.3390/ani12212907

Chapman, S., & Dobbs, P. (2023). Veterinary care of ageing animals in zoos: Description of a proactive approach. In *Optimal wellbeing of ageing wild animals in human care* (pp. 107–121). Springer International Publishing. https://doi.org/10.1007/978-3-031-30659-4_8

Collins, C., McKeown, S., & O'Riordan, R. (2023). A comprehensive investigation of negative visitor behaviour in the zoo setting and captive animals' behavioural response. *Heliyon*, *9*(6). https://doi.org/10.1016/j.heliyon.2023.e16879

De Rouck, M., Kitchener, A. C., Law, G., & Nelissen, M. (2005). A comparative study of the influence of social housing conditions on the behaviour of captive tigers (Panthera tigris). *Animal Welfare*, *14*(3), 229–238. https://doi.org/10.1017/S0962728600029390

Fazio, J. M., Freeman, E. W., Bauer, E., Rockwood, L., Brown, J. L., Hope, K., Siegal-Willott, J., Parsons, E. C. M., & Umapathy, G. (2020). Longitudinal fecal hormone monitoring of adrenocortical function in zoo housed fishing cats (Prionailurus viverrinus) during institutional transfers and breeding introductions. *PLOS ONE*, *15*(3), e0230239. https://doi.org/10.1371/journal.pone.0230239

Fernandez, E. J. (2022). Training as enrichment: A critical review. *Animal Welfare*, *31*(1), 1–12. https://doi.org/10.7120/09627286.31.1.001

Heidenreich, B. (2007). An introduction to positive reinforcement training & its benefits. *Journal of Exotic Pet Medicine*, *16*(1), 19–23. https://doi.org/10.1053/j.jepm.2006.11.005

Herron, M. E., & Shreyer, T. (2014). The pet-friendly veterinary practice: A guide for practitioners. *Veterinary Clinics: Small Animal Practice*, *44*(3), 451–481. https://doi.org/10.1016/j.cvsm.2014.01.010

Hintze, S., & Yee, J. R. (2023). Animals in flow-towards the scientific study of intrinsic reward in animals. *Biological Reviews*, *98*(3), 792–806. https://doi.org/10.1111/brv.12930

Kemp, C., Thatcher, H., Farningham, D., Witham, C., MacLarnon, A., Holmes, A., Semple, S. & Bethell, E. J. (2017). A protocol for training group-housed rhesus macaques (Macaca mulatta) to cooperate with husbandry and research procedures using positive reinforcement. *Applied Animal Behaviour Science*, *197*, 90–100. https://doi.org/10.1016/j.applanim.2017.08.006

Laule, G. E., Bloomsmith, M. A., & Schapiro, S. J. (2016). The use of positive reinforcement training techniques to enhance the care, management, and welfare of primates in the laboratory. *Training Nonhuman Primates Using Positive Reinforcement Techniques*, 163–173. https://doi.org/10.1207/S15327604JAWS0603_02. ISBN 9780203764558.

Leeds, A., Elsner, R., & Lukas, K. E. (2016). The effect of positive reinforcement training on an adult female western lowland gorilla (Gorilla gorilla gorilla) rate of abnormal and aggressive behaviour. *Animal Behaviour and Cognition*, *3*(2), 78–87. https://doi.org/10.12966/abc.02.05.2016

Lomb, J., Mauger, A., Von Keyserlingk, M. A. G., & Weary, D. M. (2021). Effects of positive reinforcement training for heifers on responses to a subcutaneous injection. *Journal of Dairy Science*, *104*(5), 6146–6158. https://doi.org/10.3168/jds.2020-19463

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: Published in Affiliation with the American Zoo and Aquarium Association*, *16*(1), 71–83. https://doi.org/10.1002/(SICI)1098-2361,(1997)16:1%3C71:AID-ZOO8%3E3.0.CO;2-8

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. https://doi.org/10.1016/j.applanim.2006.05.041

McDougall, P. T., Réale, D., Sol, D., & Reader, S. M. (2006). Wildlife conservation and animal temperament: Causes and consequences of evolutionary change for captive, reintroduced, and wild populations. *Animal Conservation*, *9*(1), 39–48. https://doi.org/10.1111/j.1469-1795.2005.00004.x

Melfi, V. (2013). Is training zoo animals enriching? *Applied Animal Behaviour Science*, *147*(3–4), 299–305. https://doi.org/10.1016/j.applanim.2013.04.011

Mellor, D. J., Beausoleil, N. J., Littlewood, K. E., McLean, A. N., McGreevy, P. D., Jones, B., & Wilkins, C. (2020). The 2020 five domains model: Including human-animal interactions in assessments of animal welfare. *Animals*, *10*(10), 1870. https://doi.org/10.3390/ani10101870

Narayan, E., Baskaran, N., & Vaz, J. (2017). Conservation physiology of tigers in zoos: Integrating stress physiology and behaviour to monitor their health and welfare. *Big Cats*, 35–44. https://doi.org/10.5772/intechopen.69780

Otaki, Y., Kido, N., Omiya, T., Ono, K., Ueda, M., Azumano, A., & Tanaka, S. (2015). A new voluntary blood collection method for the Andean bear (Tremarctos ornatus) and Asiatic black bear (Ursus thibetanus). *Zoo Biology*, *34*(5), 497–500. https://doi.org/10.1002/zoo.21237

Pastorino, G. Q., Brereton, J. E., Drago, F., Confalonieri, E., & Preziosi, R. (2021). Investigating the effect of social grouping on the behaviour of captive leopards. *Journal of Zoo and Aquarium Research*, *9*(2), 116–123. https://doi.org/10.19227/jzar.v9i2.548

Podturkin, A. A., Krebs, B. L., & Watters, J. V. (2023). A quantitative approach for using anticipatory behavior as a graded welfare assessment. *Journal of Applied Animal Welfare Science*, *26*(3), 463–477. https://doi.org/10.1080/10888705.2021.2012783

Pomerantz, O., & Terkel, J. (2009). Effects of positive reinforcement training techniques on the psychological welfare of zoo-housed chimpanzees (pan troglodytes). *American Journal of Primatology: Official Journal of the American Society of Primatologists*, *71*(8), 687–695. https://doi.org/10.1002/ajp.20703

Puehringer-Sturmayr, V, Bloomsmith, M. A., Whittaker, M. A., McMillan, J., Puehringer-Sturmayr, V., Fiby, M., Bachmann, S., Filz, S., Grassmann, I., Hoi, T., Janiczek, C. & Frigerio, D. (2023). Effects of food-based enrichment on enclosure use and behavioural patterns in captive mammalian predators: A case study from an Austrian wildlife park. *PeerJ*, *11*, e16091. https://doi.org/10.7717/peerj.16091

Rasmussen, E. B., Newland, M. C., & Hemmelman, E. (2020). The relevance of operant behaviour in conceptualizing the psychological well-being of captive animals. *Perspectives on Behaviour Science*, *43*(3), 617–654. https://doi.org/10.1007/s40614-020-00259-7

R Core Team. (2024). *R version 4.4.1: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Riemer, S., Heritier, C., Windschnurer, I., Pratsch, L., Arhant, C., & Affenzeller, N. (2021). A review on mitigating fear and aggression in dogs and cats in a veterinary setting. *Animals*, *11*(1), 158. https://doi.org/10.3390/ani11010158

Schapiro, S. J., Bloomsmith, M. A., & Laule, G. E. (2003). Positive reinforcement training as a technique to alter nonhuman primate behaviour: Quantitative assessments of effectiveness. *Journal of Applied Animal Welfare Science*, *6*(3), 175–187. https://doi.org/10.1207/S15327604JAWS0603_03

Shyne, A., & Block, M. (2010). The effects of husbandry training on stereotypic pacing in captive African wild dogs (Lycaon pictus). *Journal of Applied Animal Welfare Science*, *13*(1), 56–65. https://doi.org/10.1080/10888700903372069

Spiezio, C., Vaglio, S., Scala, C., & Regaiolli, B. (2017). Does positive reinforcement training affect the behaviour and welfare of zoo animals? The case of the ring-tailed lemur (Lemur catta). *Applied Animal Behaviour Science*, *196*, 91–99. https://doi.org/10.1016/j.applanim.2017.07.007

Vaz, J., McElligott, A. G., & Narayan, E. (2022). Linking the roles of personality and stress physiology for managing the welfare of captive big cats. *Animal Welfare*, *31*(1), 99–111. https://doi.org/10.7120/09627286.31.1.009

Watters, J. V. (2014). Searching for behavioral indicators of welfare in zoos: Uncovering anticipatory behavior. *Zoo Biology*, *33*(4), 251–256. https://doi.org/10.1002/zoo.21144

Weibel, C., Miller, A., Hill, N. A., Newcomer, M., & Ferrie, G. M. (2021). When a habitat becomes a home: Housing and husbandry of spotted hyenas Crocuta crocuta at Disney's animal Kingdom®. *Journal of Zoo and Aquarium Research*, *9*(1), 61–65. https://doi.org/10.19227/jzar.v9i1.435

Williams, E., Hunton, V., Hosey, G., & Ward, S. J. (2023). The impact of visitors on non-primate species in zoos: A quantitative review. *Animals*, *13*(7), 1178. https://doi.org/10.3390/ani13071178

Young, R. J., de Azevedo, C. S., & Cipreste, C. F. (2020). Environmental enrichment: The creation of opportunities for informal learning. *Zoo Animal Learning and Training*, 101–118. https://doi.org/10.1002/9781118968543.ch6