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Effects of environmental enrichment on the behaviour of zoo-housed cinereous vultures *Aegypius monachus*

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Abstract

Environmental enrichment is used to enhance the well-being of zoo-housed animals by providing a variety of stimuli and to encourage the expression of species-specific natural behaviours. This study assessed the effects of different types of environmental enrichment on the behaviour of 13 cinereous vultures *Aegypius monachus* in a zoo setting. Six enrichment items were used: large carcasses, forage boxes, twig balls, a wooden box with tubes, mirrors, and basketballs. Vulture behaviour was observed and compared between a baseline period and an enrichment period. The vultures only interacted with the large carcass and mirror enrichments, likely due to neophobia toward novel stimuli. However, we found a significant decrease in abnormal repetitive behaviours during the enrichment period, even with enrichment items that the vultures did not directly interact with. Finally, the presentation of large carcasses allowed the zoo-housed vultures to behave more naturally as they would in the wild, significantly increasing their social and locomotive behaviours. Overall, this study highlights the importance of providing optimal conditions for zoo-housed vultures, particularly given the endangered status of many species and their involvement in breeding programs aimed to boost wild populations.

Introduction

Environmental enrichment, the provision of items to stimulate the expression of natural behaviours, is widely used to improve the welfare of an animal in zoo settings (Azevedo et al. 2016). Laméris et al. (2021) stated that environmental enrichment is used to enhance an animal's environment by providing variation in stimuli or creating opportunities for choice while considering the species-specific natural behaviours. Enrichment can also increase control over the environment by allowing an animal to perform behaviours from their natural repertoire to obtain things they need to survive (Irwin et al. 2013). However, existing research on the link between environmental enrichment, behaviour and welfare of zoo animals primarily focuses on mammals (Binding et al. 2020) and lack studies on other common captive taxa like birds, including vultures. Previous studies have shown that birds of prey are often susceptible to unhealthy environmental conditions when they are faced with the inability to express their natural behaviours, which may lead to increased levels of abnormal and often repetitive behaviours like feather picking, feather chewing, screeching, and/or abnormal aggression (Hoek et al. 1998; Jones et al. 2001). Additionally, static conditions in captivity often lack the appropriate environmental stimuli found in naturalistic conditions. This can potentially result in boredom, the inability to cope with stressors, apathy, and decrease the performance of species-specific natural behaviours (Skibiel et al. 2007; de Almeida et al. 2018).

Animal care specialists and welfare management organizations emphasize that animals must actively interact with enrichment items to be able to assess the enrichment's effectiveness in improving an animal's welfare (Alligood and Leighty 2015; Mellor et al. 2020; Decker et al. 2023). Any enrichment item that does not generate successful interactions is often regarded as having an insignificant welfare benefit (Decker et al. 2023). Focusing on active interactions for evaluating enrichment may lead to misunderstandings in less-studied captive taxa, including species such as vultures. Decker et al. (2023) stated that successful interactions may not necessarily be the most effective method to evaluate welfare benefits and that items without direct interactions can nevertheless be highly beneficial for animals. Therefore, studies focused on assessing subjective well-being in relation to enrichment items may be a valuable approach for evaluating the welfare benefits of enrichment (Decker et al. 2023), such as by examining changes in abnormal repetitive behaviours with enrichment use. The use of enrichment in zoo-housed conditions may also bring a wide range of benefits to individuals destined for reintroduction, including the development of foraging skills, social group interactions, courtship and mating behaviours, habitat selection, physical conditioning, and movement skills, thereby increasing their chances of survival and success following release (Reading et al. 2013; Clark et al. 2023). A study by Tetzlaff et al. (2019) stated that captive-born juvenile black-tailed prairie dogs *Cynomys ludovicianus* exposed to live predators before translocation had a higher post-release survival than untrained conspecifics.

The current study assessed the effects of different types of environmental enrichment on cinereous vulture *Aegypius monachus* behaviour in a zoo setting. Cinereous vultures are part of the old-world vultures which are, according to the IUCN Red List of Threatened Species as of 2020, “Near Threatened” (IUCN 2021). Therefore, captive-breeding programmes have been initiated, aiming to conserve sustainable backup populations of cinereous vultures to ultimately reintroduce this species into the wild. Vultures play an essential role in ecosystems as they specialize in consuming carrion (Costillo et al. 2007). Without them, other scavengers would begin to flourish, and this could increase the risk of bacterial and viral infections spreading from carcasses to humans or other species (Costillo et al. 2007).

Therefore, it is crucial for the captive populations participating in these breeding programmes to succeed in mating and reach the goal of enlarging the wild population. Investigating the impact of enrichment on zoo-housed vulture behaviour – specifically targeting species-specific natural behaviours - may enhance their welfare, increase breeding success and support reintroduction goals, aligning with conservation goals (Reading et al. 2013). Insights from enrichment studies can help inform reintroduction programmes on which enrichment items to use for specific individuals, helping individuals develop and refine behavioural skills essential for survival in the wild (Reading et al. 2013).

Figure 1. Cinereous vulture aviary at Zoo Planckendael.

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Materials and methods

Ethical statement

The experiments presented here adhere to all relevant Belgian and European legislation, as well as international and scientific standards and guidelines. No additional ethical approval was necessary as all interventions in this study were regarded as environmental enrichment for the animals, aligning with current European Union and Belgian animal welfare laws and zoo directives. Consequently, formal approval for this study was waived by the Royal Zoological Society of Antwerp. Enrichment items used in this research underwent evaluation and approval by the veterinarian, curator, and the keeper coordinator of Zoo Planckendael, all of whom endorsed the study. The presentation of these enrichment items allowed animals to choose freely whether to interact with them, or not.

Subjects and housing conditions

Behavioural data were collected between July 2022 and November 2022 on a group of 13 adult cinereous vultures (six females and seven males, age range one to eight years) housed in Zoo Planckendael, Belgium. The cinereous vultures were housed in an outdoor aviary of 645 m^2 with a height ranging between 6 m and 15 m. The aviary included perches, trees, stumps, logs, a variety of vegetation, rocks, a pool of 54 m^2 in size and 40 cm deep, and shelters of various sizes, the largest measuring 6 m^2 and 2.1 m in height above the ground. The vultures remained in this aviary all year, in all weather conditions (Figure 1). Prior to this study, the vultures were never presented with any novel environmental enrichment besides the permanent structures of the aviary, such as the trees, shelters, a water pool, and perches that always remained available.

Enrichment items

We selected six enrichment items that were novel to the vultures (Figure 2). These items were carefully selected to target a range of natural behaviours and enhance the complexity of the vultures' enclosure.

The first four items were focused on food-based enrichment. We presented the vultures' regular diet, including rats, rabbits, and White Saanen goat carcass in four different conditions: forage box, twig ball feeder, tube feeder and large carcass. The vultures were never presented with large carcasses and food-based enrichment prior to this study. Their regular diet was normally just presented plainly on the aviary floor. All food-based enrichments were presented on the aviary floor.

In the forage box condition, we provided two cardboard boxes (0.12 m^2) per session, each containing eight whole rats, which were open and tilted to enable the birds to access the contents.

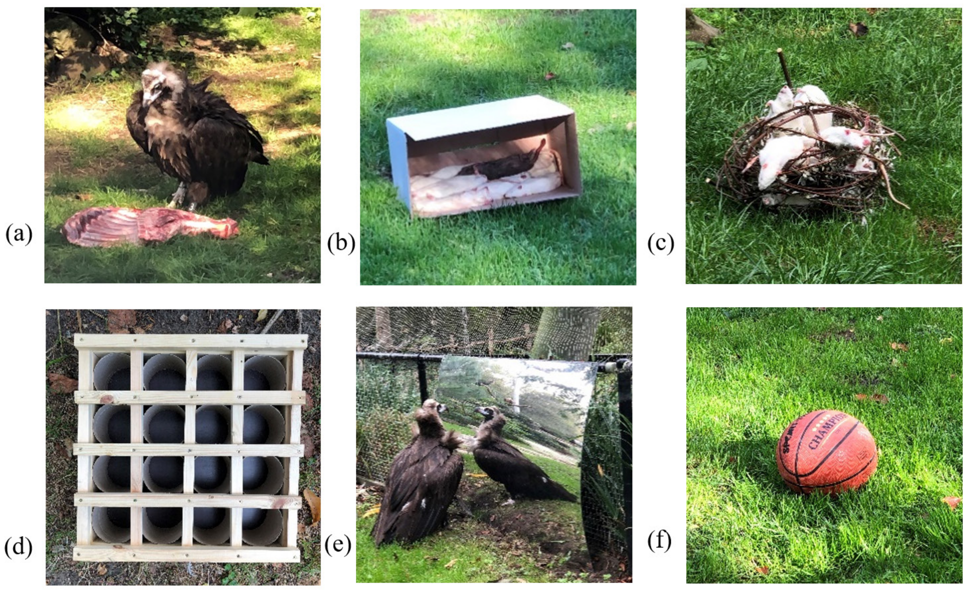

Figure 2. Environmental enrichment types provided to the cinereous vultures; (a) large carcass; (b) forage box; (c) twig ball; (d) wooden box with tubes; (e) mirror; (f) basketball.

The twig ball feeder featured two willow twig balls (diameter: 20 cm) with multiple openings, each containing six whole rats. The tube feeder included one wooden box (0.5 m^2) that contained 16 vertically oriented cardboard tubes (diameter: 6 cm), some baited with pieces of goat carcass or whole rats. In the large carcass condition, two to three whole goat carcasses of 8-12 kg were presented, compared to the 4 kg carcass pieces from their regular diet. The two remaining environmental enrichment items were not food-based: mirrors and basketballs. In the mirror condition, two shatterproof mirrors (1.5 m x 1.5 m) were strategically placed in locations where the vultures often stood or perched, and the basketballs were provided on the enclosure floor.

Procedure

This study consisted of two testing periods: a baseline period of nine days and an enrichment period of 50 days. Within the enrichment period, there were 15 control days, referred to as 'no enrichment' in this study, to assess any behavioural changes in the absence of enrichment (Figure 3).

During the baseline period, no novel enrichment items were presented. During the enrichment period, we provided the novel enrichment items to the vultures. Only one enrichment item was presented at a time, and the presentation of each enrichment item was repeated between five and seven times over the course of the enrichment period. The order of the enrichment items and "no-enrichment" control days was pseudo-randomized to avoid habituation and potential biases of other events. The large carcass remained within the enclosure for 2 consecutive days to allow the vultures to finish feeding – as they would in the wild. From September onwards, the tube feeder, mirror, twig ball and basketball, respectively, were occasionally presented on consecutive days with the intention to help overcome neophobia and promote habituation. The enrichment items were always placed at the same locations in the enclosure.

Aug-22

Monday	Tuesday	Wednesday	Thursday	Friday	Saturday	Sunday
1	2	3	4	5	6	7
Basketball	Control	Forage box	Control	Mirror		
8	9	10	11	12	13	14
	Twig ball	Control		Control		
15	16	17	18	19	20	21
	Forage box	Control		Control		
22	23	24	25	26	27	28
Forage box	Control	Mirror	Control			
29	30	31				
Large carcass	Large carcass	Control				

Sep-22

Monday	Tuesday	Wednesday	Thursday	Friday	Saturday	Sunday
			1	2	3	4
				Basketball		
5	6	7	8	9	10	11
Control	Control		Control			
12	13	14	15	16	17	18
			Twig ball			
19	20	21	22	23	24	25
Large carcass	Large carcass		Tube feeder	Tube feeder		
26	27	28	29	30		
Mirror	Mirror	Mirror	Twig ball	Twig ball		

Oct-22

Monday	Tuesday	Wednesday	Thursday	Friday	Saturday	Sunday
					1	2
3	4	5	6	7	8	9
Large carcass	Large carcass		Forage box	Twig ball		
10	11	12	13	14	15	16
Basketball	Basketball	Control	Tube feeder			
17	18	19	20	21	22	23
				Tube feeder		
24	25	26	27	28	29	30
Control			Forage box	Control		
31						
Basketball						

Nov-22

Monday	Tuesday	Wednesday	Thursday	Friday	Saturday	Sunday
	1	2	3	4	5	6
	Basketball	Mirror		Mirror		
7	8	9	10	11	12	13
			Forage box	Twig ball		
14	15	16	17	18	19	20
Tube feeder	End of study					

Figure 3. Enrichment schedule of the enrichment period August 2022 to November 2022.

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Observations

We developed an ethogram based on our pilot observations in June 2022 and existing literature, comprising 30 behaviours that were grouped into 8 behavioural categories (Table 1). For the data analysis, we classified the behavioural categories into event and state behaviours.

Using continuous focal animal sampling, each bird was observed during two five-minute observations daily, totalling ten minutes per bird per day. The total observation time for both observation periods combined was 127.8 hours. The order of the observed focal animals was randomly determined based on a list randomizer and birds were individually identifiable by their leg tags. Observations included recording how often each event behaviour, including agonistic, affiliative, and diverse, occurred, and how long each state behaviour, including body care, locomotion, stationary, feeding, and other, occurred. All behaviours are defined in the ethogram (Table 1). All observations were conducted between 10:00 h and 16:00 h, and each vulture was observed twice a day in all conditions and controls.

Weather conditions and the number of visitors were recorded in real-time before starting each focal observation session. Behavioural data were collected using the ZooMonitor app (Ross et al. 2016).

Data analysis

We summed the counts of each event behaviour (agonistic, affiliative, diverse) per subject per observation session, then calculated the frequency per hour by dividing the total count of each behaviour by the total session time in hours. For each state behaviour (body care, locomotion, stationary, feeding, other), we calculated the total duration per subject per observation session and determined the proportion by dividing the total duration of each behaviour by the total session time. For each behaviour (excluding enrichment-interaction), we created a

Table 1. Ethogram used during the study (based on Plácido et al. 2024).

Behavioural category	Individual behaviour	Description
State behaviour		
Body care	Feather preening	Moving beak over feathers to clean or realign.
	Scratching	Scratching head with feet.
	Stretch	Expanding or flexing wings or legs outward.
	Ruffle	Shaking the head, wings, body, tail, usually in one movement.
	Drying	Opening wings in full extension when wet after bathing or rain.
	Sunbathing	Open wings in direct sunlight to warm up or dry.
Locomotion	Walk	Slow steady steps, one leg in front of the other.
	Hop	A jump towards something, wings closed or open at the same time.
	Run	Fast steps, one leg in front of the other, wings can be opened or closed.
	Fly	Flapping wings to move from one spot to another or flying around enclosure, feet are off the ground.
	Flap wings	Flapping wings in place without moving feet off perch or ground.
Stationary	Standing	Upright on legs, on the ground, rocks, stump, perch, shelter, in water, other (eyes open).
	Resting	Standing in any location, with eyes closed.
	Laying	Laying on chest or on abdomen on the ground.
Feeding	Feeding diet	Tear of food and ingestion with beak (rats, rabbits, small carcass).
	Feeding enrichment	Tear of food and ingestion with beak (large carcass).
	Drinking	Lowering head to a water source, taking water with beak and lifting head upward to swallow water.
Other	Abnormal repetitive behaviour	Occur when a bird repeatedly touches a particular spot, object, or body part with the tip or side of its beak or repeatedly gnaws on the wires of the enclosure.
Event behaviour		
Agonstic	Chase	One individual swiftly pursuing another individual.
	Flee	Individual flying or running away from another aggressive individual.
	Conflict	Physical fight between two vultures which usually involves legs and beak.
	Peck	One individual aggressively touches another individual with beak.
	Kick	Claw at another individual with outstretched talons, usually involves a lunge with a jump.
	Aggressive walk	Walking slowly on the ground with head lowered and raised feathers, usually to obtain food.
Affiliation	Approaching	Walking, flying next to partner, and standing in close proximity to one another, flying to same area together.
	Greeting	Rotating the head with raised feathers, sometimes touching the head of the other vulture with the beak.
	Allopreening	Picking of neck and head feathers of another vulture (note which individual).
	Copulating	Individuals mating, male on top of female.
Diverse	Pecking substrate	Biting with beak on grass, rock, wood, etc.
	Open wings	Occurs when wind is blowing strongly.
	Vocalization	High pitched screeches.
Enrichment-interaction	Enrichment-interaction	Actively engaging with an enrichment item.

Generalised linear mixed model (GLMM) with a zero-inflated negative binomial distribution that included subject identity as a random effect to correct for repeated measures and the total observation duration per subject per session as offset to control for differential durations of the observation sessions. "Condition" (baseline, no enrichment, forage box, large carcass, tube feeder, twig balls, mirror, basketball), "weather" (cloudy, partly cloudy, rainy, sunny), and "visitors" (the number of observed visitors per focal observation) were included as main fixed factors to examine their effect on the different behaviours. We used likelihood ratio tests and Chi-square distribution to compare the full model with the null model. Diagnostic plots (residuals vs. fitted and QQ plots) were used to examine assumptions of normality and homogeneity of variances, and we tested uniformity and dispersion of the residuals using the DHARMa package (Hartig et al. 2021). All analyses were performed using R version 4.1.3 (R Core Team, 2021), with the GLMMs calculated using the glmmTMB package (Brooks et al. 2017).

Results

Activity budget

The behavioural categories with higher occurrences during the enrichment period compared to the baseline period were stationary (49%) and body care (26%). Locomotion (22%), diverse (7%), feeding (7%), and agonistic (4%) were higher in occurrence during the baseline period than during the enrichment period. Affiliation behaviour was nearly the same between baseline and enrichment period (2%).

Interactions with a given enrichment

The vultures were observed interacting with only two out of the six enrichment items: the mirror (n=16) and the large carcass (n=522).

Effects of enrichment condition on vulture behaviour

Enrichment condition significantly influenced the frequency of the event behaviours agonistic (X^2=115, df=7, P<0.001), affiliative (X^2=28.9, df=7, P<0.001) and diverse (X^2=33.7, df=7, P<0.001) (Figure 4).

Agonistic behaviour occurred significantly more often during baseline (M=4.86, SEM=0.74, all P<0.01) and large carcass (M=10.4, SEM=1.56, all P<0.001) than during no enrichment (M=1.93, SEM=0.40), basketball (M=0.24, SEM=0.14), forage box (M=1.25, SEM=0.74), mirror (M=0.69, SEM=0.27), tube feeder (M=0.28, SEM=0.21), and twig balls (M=1.52, SEM=0.62).

Affiliative behaviour occurred significantly more frequently during baseline (M=2.00, SEM=0.55, all p <0.02), large carcass (M=5.88, SEM=1.02) and no enrichment (M=1.65, SEM=0.45) than during mirror (M=0.27, SEM=0.16).

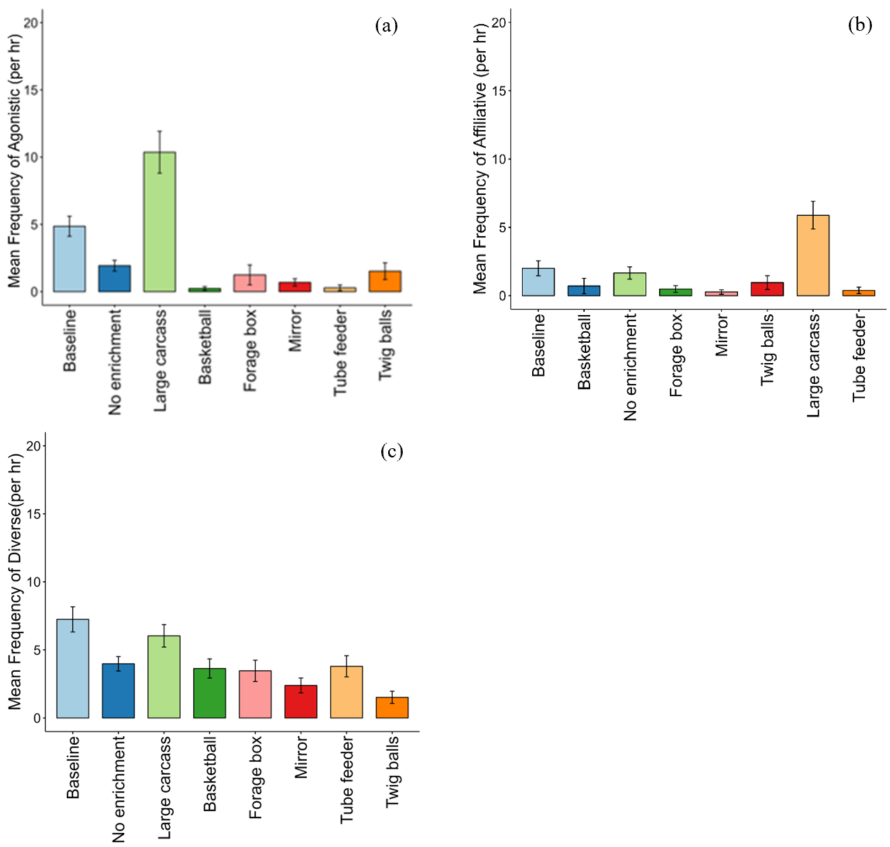

Figure 4. Mean frequency per hour showing agonistic (a), affiliative (b) and diverse (c) behaviours during each condition.

Diverse behaviour occurred significantly more often during baseline (M=7.24, SEM=0.92, all P<0.001) and basketball (M=3.64, SEM=0.71, all P<0.03) than during forage box (M=3.47, SEM=0.78) and twig balls (M=1.52, SEM=0.45). Diverse behaviours also happened significantly longer during mirror (M=2.40, SEM=0.55, P<0.04) than during twig balls.

Enrichment condition also significantly influenced the proportion of the state behaviours body care (M=14.8, df=7, P=0.04), locomotion (M=88.04, df=7, P<0.001), stationary (M=96.5, df=7, P<0.001), other (M=22.5, df=7, P=0.002) and feeding (M=14.3, df=7, P=0.04) (Figure 5).

Body care behaviours lasted significantly longer during twig balls (M=0.27, SEM=0.02, P=0.03) than during basketball (M=0.15, SEM=0.02).

Locomotion behaviour lasted significantly longer during baseline (M=0.03, SEM=0.00, all P<0.01) and large carcass (M=0.03, SEM=0.00, all P<0.07) than during basketball (M=0.003, SEM=0.00), forage box (M=0.009, SEM=0.00), mirror (M=0.009, SEM=0.00), tube feeder (M=0.008, SEM=0.00) and twig balls (M=0.01, SEM=0.00). Locomotion behaviours also lasted significantly longer during baseline period (all P<0.01) than during no enrichment (M=0.01, SD=0.00). Finally, mirror, tube feeder,

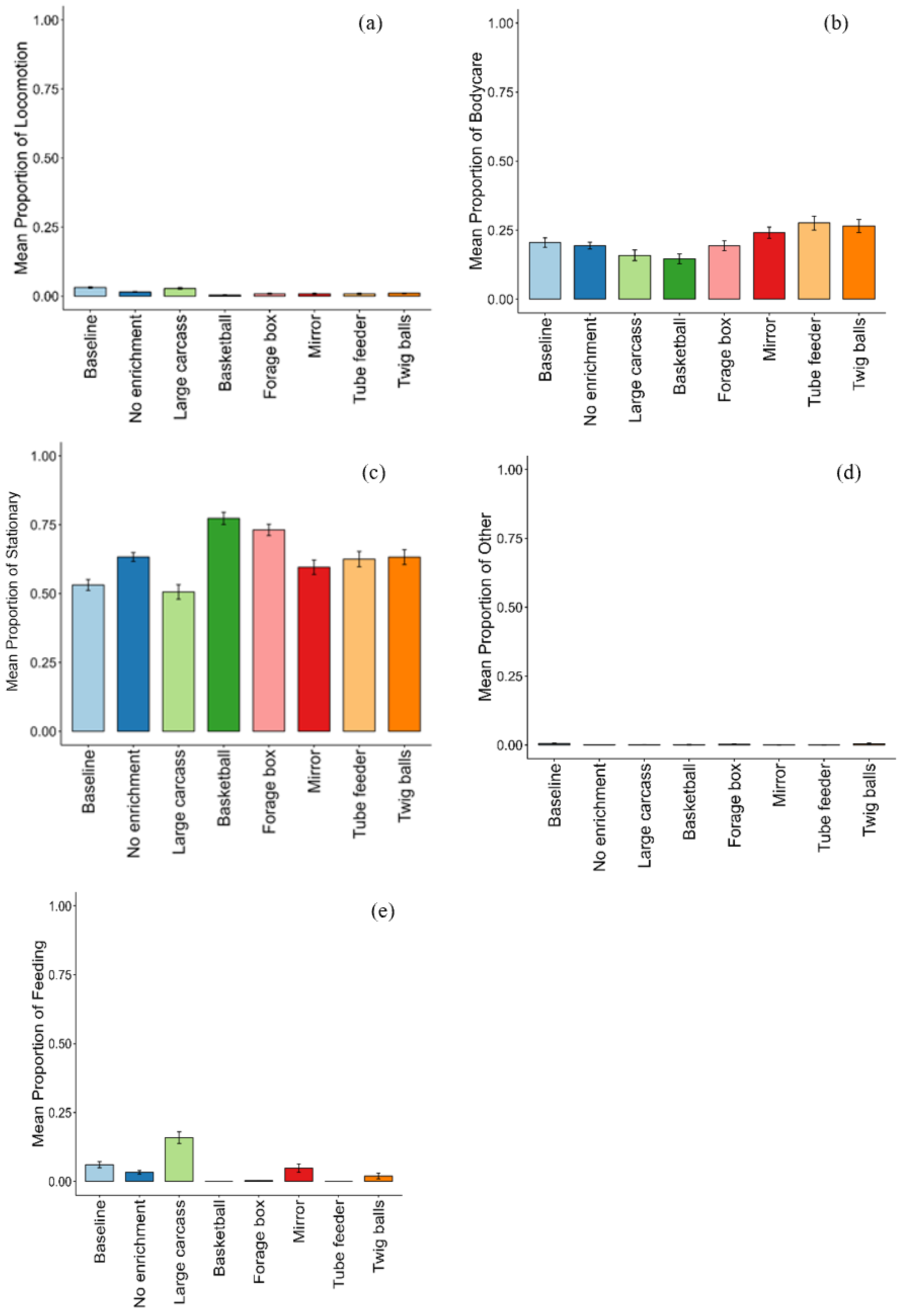

Figure 5. Mean proportion of the total session time showing locomotion (a), body care (b), stationary (c), other (d) and feeding (e) behaviours during each condition.

Table 2. The effects of weather conditions on the mean frequency per hour of agonistic and diverse behaviours (mean±SEM).

Weather	Agonistic (M±SEM)	Diverse (M±SEM)
Cloudy	2.07±0.58	4.98±0.81
Partly cloudy	2.45±0.33	4.97±0.40
Rainy	0.75±0.45	1.35±0.61
Sunny	3.62±0.54	3.38±0.41

no enrichment and twig balls (all P<0.03) had significantly longer locomotion behaviours than during basketball.

Stationary behaviour lasted significantly longer during basketball (M=0.77, SEM=0.02, all P<0.04) and forage box (M=0.73, SEM=0.02, all P<0.01) than during baseline (M=0.53, SEM=0.02), no enrichment (M=0.63, SEM=0.02), mirror (M=0.60, SD=0.03), large carcass (M=0.51, SEM=0.03) and twig balls (M=0.63, SEM=0.03). Basketball (M=0.77, SEM=0.02, P<0.04) also lasted significantly longer with stationary behaviours than during tube feeder (M=0.63, SEM=0.03). Finally, stationary behaviours lasted significantly longer during no enrichment (all P<0.03) than during large carcass and forage box.

Other behaviour lasted significantly longer during baseline (M=0.005, SEM=0.002, P=0.007) than no enrichment (M=0.001, SD=0.00).

Feeding behaviour lasted significantly longer during mirror (M=0.04, SEM=0.01, P<0.04) than forage box (M=0.002, SEM=0.001).

Effects of weather condition on vulture behaviour

We found a significant effect of weather on the event behaviours agonistic (X^2=14.8, df=3, p <0.001) and diverse (X^2=14.3, df=3, P<0.001) (Table 2).

Agonistic behaviour happened significantly more often during sunny (all P<0.05) than during partly cloudy and cloudy.

Diverse behaviour happened significantly more often during partly cloudy (P<0.02) and cloudy (P<0.01) than during rainy weather.

We also found a significant effect of weather on the state behaviours body care (X^2=18.7, df=3, P<0.001), locomotion (X^2=17.4, df=3, P<0.001), stationary (X^2=32.7, df=3, P<0.001) and other (X^2=3.71, df=3, P<0.001) (Table 3). Other behaviour showed no significant differences in pairwise comparisons between the weather conditions.

Body care behaviour happened significantly longer during cloudy than partly cloudy (P<0.02) and sunny (P<0.001) weather.

Locomotion behaviour happened significantly longer during sunny (all P<0.001), partly cloudy and cloudy than during rainy.

Stationary behaviour happened significantly longer during rainy (all P<0.01) than during cloudy and partly cloudy. Sunny (P<0.01) and partly cloudy (P<0.01) weather had significantly longer durations of stationary behaviour than cloudy weather.

Visitor effect on vulture behaviour

We found a significant effect of visitor presence on the event behaviours agonistic (X^2=5.77, df=1, p <0.001) and diverse (X^2=12.2, df=1, p <0.001). We also found a significant effect of visitor presence of the state behaviours locomotion (X^2=0.45, df=1, p <0.001), stationary (X^2=3.79, df=1, p <0.001) and other (X^2=24.6, df=1, p <0.001).

There was a positive correlation between the number of visitors and the frequency of the behaviours agonistic, diverse, and the proportion of the behaviour's locomotion, stationary and other.

Visitor presence ranged from 0 to 77 visitors per five-minute interval. The average number of visitors per five-minute interval varied by weather condition: 1.93 for heavy rain, 3.14 for light rain, 4.72 for cloudy, 6.87 for partly cloudy, and 6.94 for sunny weather conditions.

Discussion

This study assessed the effects of six different environmental enrichment items on the behaviour of zoo-housed cinereous vultures to better understand how zoos may encourage the expression of species-specific natural behaviours in vultures.

Our results indicate that the vultures only interacted with the large carcass and mirror enrichment. One possible explanation for the lack of interactions with the other items could be neophobia, which is the fear of novel and unfamiliar objects (Greenberg and Mettke-Hofmann 2001). It is important to consider that fear may be a natural response in vultures due to the risks associated with scavenging behaviours (Ellison et al. 2015), including nest

Table 3. The effects of weather conditions on the mean proportion of the total session time of body care, locomotion and stationary behaviours (mean±SEM).

Weather	Body care (M±SEM)	Locomotion (M±SEM)	Stationary (M±SEM)
Cloudy	0.28±0.02	0.02±0.00	0.56±0.02
Partly cloudy	0.21±0.01	0.02±0.00	0.61±0.01
Rainy	0.12±0.03	0.01±0.00	0.72±0.04
Sunny	0.18±0.01	0.02±0.00	0.65±0.01

predation (Cortés-Avizanda et al. 2009) and human conflict due to scavenging close to human settlements (Buechley et al. 2022). The zoo-housed vultures in the present study showed high levels of neophobia. When an enrichment item was present in their enclosure, we found that they spent more time stationary and remained on the perches compared to baseline. However, vultures are not the only species that exhibit neophobia; many mammalian and avian species also display this trait (Greenberg 2003). Therefore, habituating vultures to novel objects may be necessary to encourage exploration over time (Greenberg 2003; Miller et al. 2022).

The novelty of the enrichment items may have caused stress, as the vultures had never encountered them before, causing the unfamiliar objects to disrupt their daily repetitive schedules they have grown accustomed to. A potential way of handling stress is by engaging in stress-relieving displacement behaviours such as body care behaviours. Our results show that the vultures spent more time performing body care activities when the novel item twig balls were present in the enclosure. Preening has been identified as a way for birds to relieve stress and anxiety while also maintaining hygiene (Kozak et al. 2019). Delius (1988) described that when pigeons were exposed to stressful environments, they increased their preening behaviour and found similarities between displacement behaviours in birds and those observed in mammals, such as preening, grooming, yawning, and stretching.

Nonetheless, given the lack of research on zoo-housed vultures, it is important to consider that these birds may require longer habituation periods to overcome their neophobia due to their natural fearfulness (Ellison et al. 2015). Short-term exposure to novel items may cause stress in vultures, but long-term exposure and frequent rotation of enrichment items can lead to habituation and diminish neophobic behaviours (Greenberg 2003; Fox and Millam 2007; Fairhurst et al. 2011; Ellison et al. 2015; Miller et al. 2022). The habituation process might involve prolonged exposure to a novel stimulus, which could unintentionally flood the animals with an unavoidable presence. It is advisable to be cautious and consider incorporating a training process in which the new item is paired with something positive for the animals, such as food rewards, to potentially facilitate desensitization. This gradual acclimation method helps the animal associate the novel item with positive experiences, promoting more effective habituation and reducing potential stress responses.

The vultures' interactions with the mirrors demonstrate that despite a lack of prior exposure, they can overcome neophobia by approaching enrichment items with curiosity and exploratory behaviours. Therefore, once the initial period of neophobia is overcome, it is possible that the enrichment items may benefit the birds' welfare in a zoo setting by providing variation to their repetitive daily routines, increase their ability to cope with stress and their motivation to perform species-specific behaviours more frequently. When examining whether novel enrichment can reduce stress in a captive population of wild-caught Clark's nutcrackers *Nucifraga columbiana*, Fairhurst et al. (2011) also found that short-term exposure increased stress whereas long-term exposure was less stressful due to acclimation, suggesting physiological benefits.

Decker et al. (2023) suggested that even if animals do not directly interact with enrichment items, neophobic stress can nevertheless still be reduced and improve well-being by allowing them choice and control over their environment. Even though the vultures in the present study did not interact with all the enrichment items, it is possible that these items had a positive indirect effect on their behaviours. Another factor to consider is that the vultures may have been unable to cope with some of the novel items and the potential stress associated with their introduction due to the static conditions they have grown accustomed to in captivity, including consistent repetitive feeding schedules and placement of food in the enclosure, fixed enclosure layout with minimal variability, limited flight space and absence of natural threats. When unexpected novel enrichment is exposed to the vultures, it may increase stress as they are not accustomed to change and novelty. However, previous studies have stated that mild stressors, such as the introduction of novel items, may be enriching for vultures by potentially expanding their ability to cope with stressors and changes in their environment, thereby increasing their adaptability (Veissier et al. 2024). This increased adaptability may be beneficial for individuals destined for reintroduction, as it may help increase an animal's resilience, increasing its chances of survival and success after release (Reading et al. 2013; Clark et al. 2023). This is why it is critical to consider the long-term effects of using enrichment items with zoo-housed vultures.

Our study emphasizes the importance of enrichment even when there is little to no direct interactions. This is suggested by a significant decrease in abnormal repetitive behaviours (category: 'Other') during the no-enrichment control days throughout the enrichment period, compared to the baseline period.

The vultures were commonly observed performing abnormal repetitive behaviours throughout both periods. These behaviours occur when a bird repeatedly touches a particular spot, object, or body part with the tip or side of its beak (Hoek et al. 1998) or repeatedly gnaws on the wires of the enclosure (Echols 2010; Mellor et al. 2018). The zoo-housed cinereous vultures of the present study often perched on the wired mesh and continuously pecked, pulled, and gnawed the wire with their beaks and talons for up to 15–20-minute intervals. This may indicate inappropriate rearing or housing conditions in zoo-housed birds (Hoek et al. 1998), and potentially boredom due to a lack of variability in stimulation. The significant decrease in these repetitive behaviours during the enrichment period demonstrates the promising potential of enrichment and the importance of taking indirect effects into account. Long-term exposure to and frequent rotation of enrichment items may improve their overall well-being in zoo settings.

The presentation of large carcasses is important because it potentially allows zoo-housed vultures to behave naturally, as they would in the wild. We found three main behaviours that were significantly improved by large carcass enrichment. First, the frequency of agonistic and affiliative behaviours increased more than twofold during the large carcass condition compared to the other conditions and the smaller carcasses fed during the baseline condition. Vultures are known for their highly social nature, emphasising the importance of providing captive environments in which they can engage in their natural social behaviours (Overveld et al. 2020). This is consistent with research suggesting that gatherings at carcasses in the wild play an important role in vulture socialisation and interactions, particularly outside the breeding season (Overveld et al. 2020). The vultures in the present study included potential breeding pairs that simultaneously arrived at the large carcass enrichment, greeted each other and co-fed on the carcass together. At the same time, the vultures acted aggressively towards other individuals to protect the large carcass they were co-feeding on. These results suggest that gatherings near large carcasses may be useful for identifying potential breeding pairs, as large carcasses encourage natural sociability (Bildstein 2022), and for studying their social behaviours both with each other and with conspecifics. Additionally, such observations may contribute to breeding programs aimed at ensuring successful mating and the reintroduction of captive-born offspring into the wild, thus helping to bolster threatened wild populations.

Second, the vultures were more active during baseline and the large carcass enrichment compared to the other enrichment conditions. This is likely because the vultures interacted with the large carcass the most and exhibited less neophobia towards it compared to the other items. The large carcass may enable the vultures to express more natural feeding behaviours in zoo-housed conditions, by encouraging them to fly from the perches to the ground of the enclosure, explore and increase movement activity. As demonstrated by Fluhr et al. (2021), free-ranging griffon vultures *Gyps fulvus* exhibited a 67% increase in activity while on the ground compared to when perched. Additionally, large carcasses require more handling time due to their thicker skin and larger pieces of meat, occupying vultures longer than the small carcasses, especially as their larger beaks and talons allow them to spend more time tearing into larger carcasses compared to other vulture species (Moreno-Opo et al. 2020; Linde-Medina et al. 2021). Gaengler (2013) found that larger carcasses kept zoo-housed Andean condors *Vultur gryphus* occupied for longer periods compared to smaller carcasses. Similarly, Brereton et al. (2021) reported that providing carcasses as enrichment led to southern ground hornbills *Bucorvus leadbeateri* spending more time on feeding and food manipulation activities. Therefore, including large carcasses in vulture diets is useful. Nevertheless, the weekly diet should still include a variety of carcass types and sizes (e.g. rabbits, rats, etc.), as well as larger carcasses, to avoid boredom, since studies have shown that cinereous vultures can adapt their food preferences and feeding habits (Costillo et al. 2007).

Third, our findings show that behaviours in the category 'diverse', including vocalisations, occurred more frequently in both the baseline and large carcass conditions compared to the other conditions. This increase may be due to heightened social interactions among the vultures during feeding and higher levels of locomotive activity. Given that vultures are naturally social creatures, it is possible that the increased activity around large carcasses resulted in more vocalisation. Romani et al. (2022) highlighted the importance of vocal communication in vulture social and foraging dynamics.

External environmental conditions, such as different weather conditions and seasons, can influence vulture behaviours (Fluhr et al. 2021), as shown by our results. This is important to consider, as the vultures were housed in Belgium with a temperate maritime climate, and the study extended from July to mid-November. There was a higher occurrence of body care behaviours during sunny and cloudy weather than rainy weather. This aligns with a previous study of long-billed vultures *Gyps indicus*, where sunbathing as one of the individual behaviours of body care occurred more during sunny weather or sunny spells than during cloudy days (Yavad et al. 2018). Vultures naturally sunbathe often as they are endothermic and will possibly warm themselves and maintain body temperatures by absorbing solar radiation (Yavad et al. 2018). The colder seasons may also potentially influence the amount of time spent on self-maintenance activities, as vultures were observed to spend more time sunbathing in cold weather to increase body temperatures (Yavad et al. 2018). Additionally, our findings show that stationary behaviours lasted longer in rainy weather, while locomotive behaviours lasted longer in sunny and partly cloudy weather. The increased activity may also explain the increase in social behaviours during sunny weather. This is consistent with a study that found free-ranging vultures travelled longer distances and fed three times more frequently in the spring and summer due to the difficult foraging conditions caused by shorter days and less favourable weather in the winter (Arkumarev et al. 2021). Our results show that rainy weather diminished abnormal repetitive behaviours compared to sunny weather, most likely because the vultures were more stationary during rainy weather and remained perched in the trees, avoiding the ground and wired-mesh enclosure.

Zoo animals may also be influenced by visitors, and this phenomenon is defined as the visitor effect (Sherwen and Hemsworth. 2019). We examined whether the visitor effect had any impact on current vulture behaviour. Studies have shown that the visitor effect may have a positive, negative, or neutral impact on zoo-housed animals (Blanchett et al. 2020; Rose et al. 2020; Tay et al. 2023). Our results indicate a positive correlation between the number of visitors present and the expression of certain behaviours. It is possible that the presence of visitors may be stimulating and even beneficial to vultures, as evidenced by the increased social and locomotive/exploratory behaviours with increased visitor presence. It is also possible that visitor numbers increased when the vultures were actively interacting with the large carcass and mirror enrichment, drawing the attention of visitors. This factor should be considered in future studies, where the average number of visitors could be analysed in relation to different enrichment items present in the animals' enclosure. By examining how various enrichment items influence visitor engagement, researchers can gain insights into the potential impact of enrichment on both animal welfare and visitor experience.

Abnormal repetitive behaviours also increased with higher visitor presence, which may indicate a negative welfare state due to the visitor effect. From personal observations, the vultures appeared well habituated to visitors. They did not shy away from close-range interactions and remained perched on the wired enclosure, drawing more visitors without actively fleeing. Previous studies have found no evidence of a visitor effect on bird behaviours, although they noted changes in enclosure use, such as movement away from visitor pathways in walk-through enclosures (Blanchett et al. 2020; Rose et al. 2020). Research into animal behaviour, including the visitor effect as an independent variable, must also consider temporal and climatic changes (Rose et al. 2020), as weather may be a stronger influence on both animal behaviour and visitor presence. In the current study, we found that visitor numbers increased with changes in weather, with higher averages during partly cloudy and sunny conditions compared to rainy conditions. There was also an increase in agonistic, locomotion, diverse, other, and stationary behaviours during sunny and cloudy weather conditions. Therefore, weather may influence both visitor presence and vulture behaviour, individually and simultaneously.

The sequence used to present the enrichment items was not perfectly balanced, which presents a limitation to the study. This imbalance may have, at least theoretically, influenced the results, as certain items were presented on consecutive days. However, the decision to present the large carcass for two consecutive days per occasion was made with the aim to allow the vultures to exhibit natural behaviours, aligning their feeding habits with those in the wild. Moreover, as the vultures did not completely consume the large carcass on the first day, this approach not only ensured that they obtained adequate nutrition throughout the study but also aligned with the zookeepers' preferences.

It was also not always feasible for the zookeepers to replace enrichment items daily due to logistical constraints. Nevertheless, this presented an opportunity to explore whether the presentation of enrichment items on consecutive days – rather than spreading the sessions out over non-consecutive days – could facilitate habituation and help overcome neophobia. Future studies should consider these differences in enrichment scheduling and consider examining more closely whether there is a difference in the vultures' behaviours based on whether items are presented on consecutive days or not.

Given the exploratory nature of our study, we feel that such deviations from a strictly balanced presentation of enrichment items are justifiable. Such considerations highlight the complexities of studying the usefulness of enrichment with zoo-housed vultures and underline the importance of flexibility in experimental designs to address practical constraints. Despite its limitations, we consider the present study as a first exploratory case study, and we are confident that it provides valuable new insights and lays the foundation for future research on the use of enrichment and the welfare of less-studied zoo-housed animals.

Overall, while perfectly replicating wild conditions may not be possible in zoos, providing optimal conditions for zoo-housed vultures is crucial, particularly given the endangered status of many species and their involvement in breeding programmes aimed at boosting wild populations. Zoo-housed vultures remain highly understudied, and more research is needed to better understand their behaviours and requirements in order to achieve optimal welfare in captivity. Continued research should explore the long-term effects of enrichment items on vulture behaviour, considering their natural species-specific behaviours, to enhance understanding of zoo-housed welfare and contribute more effectively to wildlife conservation efforts. Therefore, when selecting enrichment items, it is essential to understand the species in question and to base choices on the species-specific behaviours and needs, ensuring that natural behaviours are encouraged, such as foraging and social interactions, which are critical for maintaining the physical and psychological health of zoo-housed species. Failing to address these crucial points may lead to behaviours that are counterproductive to welfare goals, such as disinterest, stress, and potentially increased abnormal repetitive behaviours. Finally, it is important to consider the indirect effects of enrichment and external influences on vulture behaviour. Solely focusing on active interactions for evaluating enrichment may lead to misunderstandings and biases, particularly regarding less-studied captive animals such as vultures.

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