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The human-animal relationship in zoo-housed mammals: Behavioral and physiological responses to visitor and keeper interactions

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Abstract Human-animal relationships (HARs) and interactions strongly influence animal welfare. Thus, advocating for positive HAR is essential for maintaining positive physical and mental health. In particular, zoo–housed species not only are exposed daily to unfamiliar humans (visitors) but also need to routinely interact with zookeepers, veterinarians, trainers, and other staff. In contrast to those in livestock and companion animals, HARs in zoos have not been extensively studied, although it is known that negative interactions can elicit stress-related behavioral and physiological responses. The present review aims to address the importance of positive HAR in wildlife species under human care. The main behavioral and physiological responses to interactions with familiar and unfamiliar humans will be discussed for a wide range of species (because HARs can also be influenced by animal-related factors). Moreover, potential alternatives to address and promote positive HAR in zoo-housed animals (e.g., environmental enrichment and positive reinforcement training) will be addressed. The HAR is part of the Five Domains Model of Animal Welfare. Therefore, recognizing that caregivers/medical staff and visitors' presence can affect an animal's emotional state is important for establishing beneficial relationships for wildlife under human care.

Keywords: keeper-animal relationship, visitor-animal interaction, social enrichment, positive reinforcement training

1. Introduction

Zoos, as an institution dedicated to the conservation and protection of wild species in captivity, relies on high standards of welfare to ensure the physical and mental health of animals (Sherwen and Hemsworth 2019; Escobar-Ibarra et al 2021; Mota-Rojas et al 2022b). Within this standard, human-animal relationships (HARs) are a key element since modern zoological institutions receive more than 700 million visitors as one of the features of zoos (Melfi and Hosey 2019; Holmes et al 2020). Moreover, zoo-housed animals are exposed to keepers and/or veterinarians as part of their daily routine, increasing the importance of nurturing HARs (Bacon et al 2021; Thomas et al 2022).

HAR can be defined as "the degree of relation or distance that exists between an animal and a human being, perceived, developed, and expressed through their mutual behavior" (Mota-Rojas et al 2020). The interaction between humans and animals encompasses any situation of any nature in which there is an interchange between two species (Sterman and Bussert 2020). The HAR has been incorporated into the five domains model of animal welfare (Mellor et al. 2020) because, depending on the animals' emotional experience, they can be classified as positive, negative, or neutral (Patel et al 2019; Hunton et al 2022).

In contrast to those in livestock and companion animals, HARs in zoos, particularly those interacting with keepers, have not been extensively studied (Sherwen and Hemsworth 2019). However, available reports on mammalian species, such as great apes (Behringer et al 2022), elephants (Brown et al 2019), ungulates (Williams et al 2021a), and carnivores (Kiranaputri et al 2021), have shown that interactions with zookeepers and visitors strongly influence behavioral and physiological responses. For example, a high number of visitants has been associated with increased activity and vigilance in zoo-housed Sulawesi crested macaques (*Macaca nigra*) (Dancer and Burn 2019) and a greater frequency of displacement behaviors (yawning) in East Javan langurs (*Trachypithecus auratus*) (Roth and Cords 2020). Furthermore, increases in cortisol (CORT) metabolites due to fear reactions to keepers were reported in rhinos (*D. bicornis michaelii* and *minor individuals*) (Carlstead 2009).

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In contrast, other studies emphasize the positive and neutral effects of both keepers and visitors of meerkats (*Suricata suricatta*) (Williams et al 2021b) and grevy zebra (*Equus grevyi*) (Miller et al 2021) and a generally reduced stress response (lower corticoid levels, reduced stereotypies, and affiliative behavior with human and nonhuman partners) (Carlstead and Brown 2005; Thomas et al 2022). Due to the current debate regarding HAR repair in zoo animals, the present review will address the importance of positive HAR repair in wildlife under human care. The main behavioral and physiological responses of known and unknown humans will be discussed, and potential alternatives, such as environmental enrichment and positive reinforcement training, will be used to address and promote positive HARs in zoo-housed animals.

2. Importance of positive human-animal relationships in zoo-housed animals

Zoos has five primary goals: 1) Conservation, 2) Education, 3) Research, 4) Animal welfare, and 5) Entertainment (D'Cruze et al 2019; Escobar-Ibarra et al 2021). Although the first four aims are considered the most important, more than 700 million people visit zoos worldwide as a form of entertainment to enjoy seeing wild species close together (Holmes et al 2020). While this is a positive trait that encourages public interest in nature and wildlife, it also means that zoo-housed animals need to face several HARs due to the presence of familiar (animal care staff, including keepers, trainers, and veterinarians) and unfamiliar (visitors) humans (Baker and Farmer 2023).

Positive, negative, and neutral relationships develop as a result of interactions with keepers, veterinarians, and visitants (Patel et al 2019; Hunton et al 2022). A positive relationship is where humans cause positive emotional responses in a species. A negative interaction is where animals show fear and avoidance toward humans, while neutral interactions are where human presence does not cause consequences for animals (Sherwen and Hemsworth 2019; Menor-Campos et al 2023; Mota-Rojas et al 2023a,b). Considering the five domains of animal welfare proposed, whether an interaction has positive or negative impacts on welfare is strongly influenced by the type of HAR (Mellor et al 2020). For example, poor welfare and a negative mental state can be elicited in zoo animals when the HAR causes fear (Sherwen and Hemsworth 2019). This phenomenon is often observed when visitors perform negative behaviors such as banging or shouting in front of an animal enclosure, as observed in Humboldt penguins (*Spheniscus humboldti*), lion-tailed macaques (*Macaca silemus*), and Sumatran tigers (*Panthera tigris sumatrae*) (Collins et al 2023). Conversely, high levels of welfare can result when human interaction acts as enrichment and people are considered symbionts (Learmonth 2019), as reported in North American clouded leopards (*Neofelis nebulosa*), in whom Wielebnowski et al. (2002) found a negative correlation between the number of hours keepers spent with leopards and corticoid concentrations.

Most animal species exhibit a natural fear of humans, but the degree or intensity of this emotion depends on the species, past experiences, and evolutionary factors (Sherwen and Hemsworth 2019). For zoo-housed animals, the keeper–animal relationship (KAR) is a source of repeated interactions and the first approach to humans (Bacon et al 2021). This relationship can evolve into a bond when it is reciprocal and beneficial for both, which is the ultimate goal of HAR for zoo-housed animals that are exposed daily to human caregivers (Thomas et al 2022). A positive keeper-animal relationship (KAR) is considered to be beneficial for the welfare of a species by reducing stress due to interactions with humans near their enclosure. A positive KAR also allows keepers to identify negative behavioral changes in animals that might be related to a health problem or environmental discomfort (Rose et al 2020). This bond and companionship are essential because the zoo staff is responsible for the animal's welfare and health by performing husbandry practices, training sessions, and simulated or actual medical exams to perform preventive medicine for the species.

Medical care and other procedures are frequently associated with stress in domestic (Dreschel 2010; Domínguez-Oliva et al 2021) and captive animals (Coleman et al 2023). According to Carlstead (2009), in a study including 219 animals of different species, such as black rhinos (*Diceros bicornis michaelii* and *minor*), cheetahs (*Acinonyx jubatus jubatus*), and maned wolfs (*Chrysocyon brachyurus*), 40% were fearful of veterinarians and medical revisions. This represents a significant risk for the animal itself and the personnel. On the one hand, physiological alterations start after the "fight-flight response" (defined as a sympathetic physiological response triggered when exposed to a threat) is activated, and other severe complications, such as immunocompromise when exposed to chronic stress and disease susceptibility, can occur (Mota-Rojas et al 2022a; Mangiaterra et al 2022). The integrity of personnel is at risk when captive wildlife exhibit unpredictable behaviors. This makes animal handling, medical examination, and training challenging because animals might associate humans with a negative stimulus, and this factor highly influences future interactions (Duncan et al 2022; Carroll et al 2022).

The mentioned interactions include the exposure of wildlife under human care to visitors as a part of their daily routine. Visitors to most worldwide zoos serve as financial support for zoological institutions (Rose et al 2020; Learmonth 2020). Animal-visitor interactions (AVIs) can be classified as "direct contact" (e.g., feeding, holding, petting) or "indirect contact" (e.g., viewing, scattering food for animals, participating in cognitive enrichment) (Learmonth 2020). A study by D'Cruze et al. (2019) involving 1241 facilities (including zoos and aquariums) reported that 75% (929) of the participants engaged in at least one type of animal-visitor interaction, and 47% (587) engaged in more than one type of interaction. Among the activities where visitors can participate, 45% correspond to petting, 33% to walk/swim through, 30% to perform, 28% to nonhand feeding, 23% to hand feeding, 8% to drive through or cage dives, and 5% to ride and walk with (D'Cruze et al 2019).

AVI in zoos, regardless of the type, incites interest in wildlife, particularly nonhuman primates, great apes, large carnivores and herbivores (Howell et al 2019), and this can lead to proconservation attitudes and interest in zoo animal welfare (Learmonth 2020). Nonetheless, several studies have shown that visitors can be stressors because of their number, noise, and activity level (Roth and Cords 2020). Therefore, HAR formation in zoo-housed animals requires evaluation methods to determine the impact that human presence has on the animals and the degree to which these relationships affect them (Learmonth 2020) to identify shortcomings and make appropriate changes to improve the welfare of captive species (Edes and Hall 2023). Figure 1 summarizes the additional, visitor-, and animal-related factors that influence HAR formation and will be discussed in the next sections.

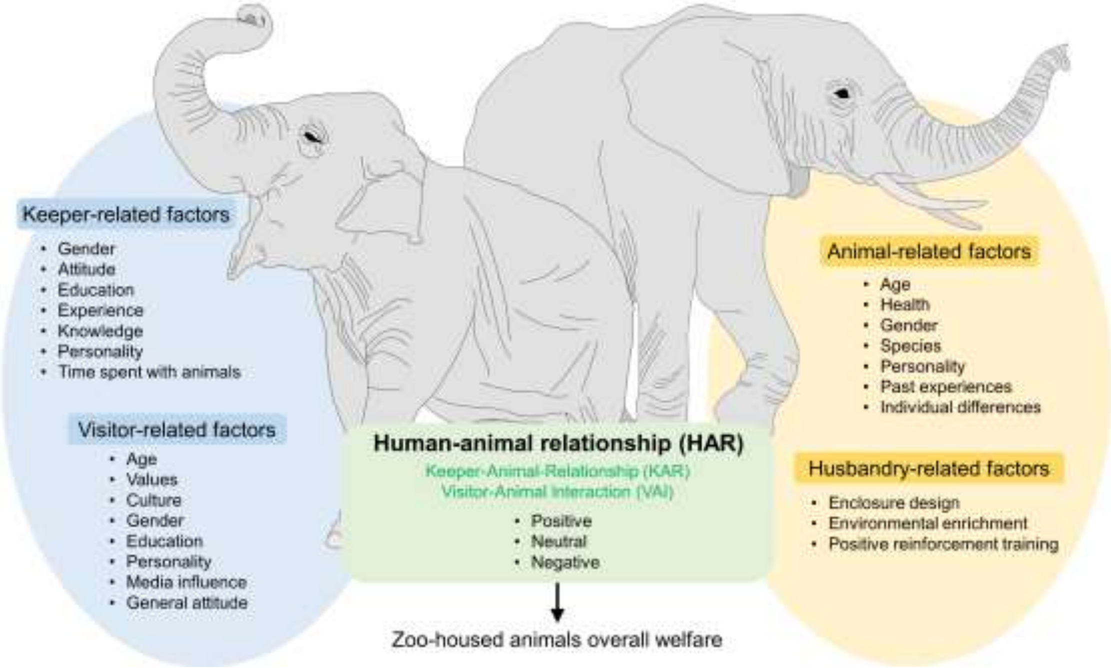

Figure 1 Elements that influence the human-animal relationship in zoo-housed species.

3. Current methods for evaluating human-animal relationships and their associations with animal welfare

Captive wildlife under human care are exposed to several external and internal stimuli that can be perceived as stressors and elicit behavioral and physiological changes as a coping mechanism (Bastian et al 2020; Hambrecht et al 2021; Domínguez-Oliva et al 2022; Mota-Rojas et al 2022b). Since stress is a complex state in which an organism's homeostasis is threatened—and might be triggered by HARs—these changes serve as short-term adaptive responses of animals and contribute to stress resilience, as reported in capuchin monkeys (*Sapajus* spp.) in whom restlessness and self-protection are considered coping strategies (Ferreira et al 2016). However, when the stimulus is prolonged or excessive and leads to distress, biological function is adversely compromised (Hambrecht et al 2021).

These responses, also known as "animal-based parameters", can be used to evaluate the impact of HAR on the overall welfare of zoo-housed animals (Cole and Fraser 2018; Sherwen and Hemsworth 2019). These indicators include variables directly measured in animals (e.g., health and physiological parameters, behavioral changes, and physical appearance) (Manteca et al 2016). Among the physiological changes triggered by distress or negative HARs, the most frequently used biomarkers are glucocorticoids (GCs) (e.g., cortisol [CORT]) (Manning et al 2022), which are produced by the activation of the sympathetic nervous system (SNS) and the hypothalamic–pituitary–adrenal axis (HPA axis) (Hambrecht et al 2021). Figure 2 describes the influence of negative HAR and endocrine changes due to the activation of the HPA axis, catecholamine release by the sympathetic-adrenomedullary axis in gorillas and catecholamine action when the system reaches circulation.

In contrast to domestic animals, in which plasma glucocorticoid levels are the gold standard for quantifying CORT concentrations (Durosaro et al 2023), for zoo-housed species, noninvasive measurements such as those of CORT metabolites in feces, urine, saliva, and hair/fur are preferred because they do not require chemical supplementation or extensive human management (Pokharel et al 2021; Gholib et al 2021; Manning et al 2022). Fecal glucocorticoid metabolites (fGCMs) are the most commonly used type of sampling because they can be easily collected from captive species, can represent the hormone concentration over time, and are less sensitive to diurnal fluctuations (Fink et al 2021). They have been used as stress-related biomarkers in

African lions (*Panthera leo bleyenberghi*) (Serres-Corral et al 2021), Asians (*Elephas maximus*) and African elephants (*Loxodonta africana*) (Brown et al 2019). Urine and salivary CORT were applied in research on golden snub-nosed monkeys (*Rhinopithecus roxellana*) and bonobos (*Pan paniscus*), respectively (Behringer et al 2022), while hair steroid hormones were measured in Asian elephants (*E. maximus*) (Pokharel et al 2021) and polar bears (*Ursus maritimus*) (Hein et al 2021). Nonetheless, when GCs are used as endocrine indicators of health and welfare, factors such as diurnal variations in serum CORT concentrations must be considered (Bechert et al 2021). Moreover, GC release responds to both negative stress, fear, and pain and positive arousal, anticipation, excitement, and reproductive stage (Hambrecht et al 2021).

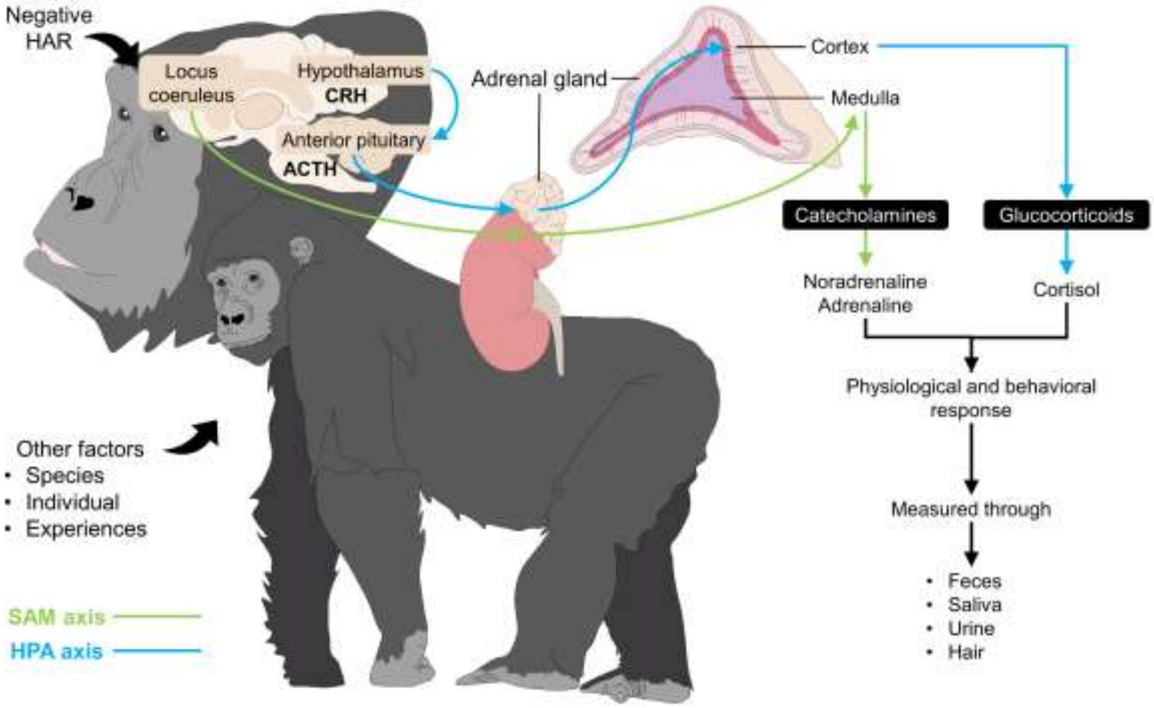

Figure 2 Stress response related to negative human-animal-relationship in wildlife under human care. Stress is the main consequence of a negative HAR. When animals perceive a threat, the HPA and SAM axes release glucocorticoids and catecholamines, respectively. The release of cortisol is the main biomarker used to evaluate the interaction of animals with zookeepers and visitors, and high concentrations of cortisol are associated with negative HAR. ACTH: adrenocorticotropic hormone; CRH: corticotropin-releasing hormone; HAR: human-animal relationship; HPA: hypothalamic–pituitary–adrenal; SAM: sympathetic adrenomedullary.

The neutrophil/lymphocyte (N/L) ratio is another parameter used to assess acute stress conditions in zoo-housed animals, such as the Sumatran tiger (*Panthera tigris sondaica)* (Kiranaputri et al 2021). The oxytocin (OXT) concentration in lowland gorillas (*Gorilla gorilla gorilla*) has been linked to affiliative interactions with conspecifics (Leeds et al 2020). Other markers can include catecholamines (e.g., epinephrine and norepinephrine) and proinflammatory mediators (interleukin-6 and tumor necrosis factor-alpha); however, these agents are not frequently evaluated as glucocorticoids (Edes et al 2023).

Behavioral assessment of stress is an extensive research field in which most current studies have been performed. In general, the so-called "visitor effect" in zoo animals has been related to negative behavioral outcomes, such as a decrease in affiliative and maintenance behaviors (Rose et al 2020) and an increase in aggressive interactions with conspecifics and humans, as reported in orangutans (*Pongo pygmaeus*) (Sherwen and Hemsworth 2019). Nonetheless, other studies have reported no differences in enclosure use, vigilance, or travel in Palawan binturongs (*Arctictis binturongs*) (Finch et al 2022), and in some other instances, the presence of visitors has a positive effect on animals, as observed in meerkats (*Suricata suricatta*) (Williams et al 2021b).

Although the evidence shows that behavioral evaluation of wildlife under human care is almost routinely performed in zoos, its evaluation can be subjective (Manning et al 2022) and challenging due to the different taxa (Rose et al 2020). Furthermore, the behavioral repertoire of captive wildlife depends on animal traits (e.g., species, genetics, personality, temperaments, past experiences) and environmental elements (e.g., social groups, enclosure, environmental temperature) (Sherwen and Hemsworth 2019). Knowledge of the biology and personality of zoo-housed animals is essential for predicting the social interactions they can form with conspecifics and keepers, as shown in Elephants by Williams et al. (2019). Therefore, to perform a comprehensive evaluation of HARs at zoological institutions, the suggested approach is to consider both physiological and behavioral changes.

4. Human-animal relationships with zookeepers and veterinarians

Although zookeepers perform daily interactions with animals and the type of bonding can impact animal response to visitors or further management, to the best of our knowledge, KAR has limited use (Thomas et al 2022). However, the quality of KAR strongly influences the reactions of animals to humans. A survey of 144 zookeepers revealed that 75.9% of respondents worked with multiple taxa and that 48.8% reported having a stronger bond with mammals. A total of 88.9% of the zookeepers mentioned a kind of bond with the zoo animal in their care, and 59.72% responded that bonding with zoo animals helps to decrease the animals' stress and facilitates husbandry procedures (Thomas et al 2022). Similarly, KAR was assessed by Melfi et al. (2022) using a modified version of the Lexington Attachment to Pets Scale to determine the strength of the bond between 187 zookeepers and mammalian species (primates, carnivores, and ungulates). The authors found that zookeepers formed bonds with the zoo species but reported stronger attachments to their companion animals.

4.1. Behavioral and physiological responses of zoo-housed animals to KAR

To maintain a positive KAR, the consistency and familiarity of keepers; their attitudes, personalities, knowledge, experience, and even facility design influence zookeeper–animal bonds (Cole and Fraser 2018). This phenomenon was reported in black rhinoceros (*D. bicornis*), Chapman's zebra (*Equus burchellii*), and Sulawesi crested black macaques (*Macaca nigra*) by Ward and Melfi (2015). The study highlighted the importance of knowledge and experience about the species since this factor can alter the latency of the animals to respond to a command. In particular, rhinos had an altered latency to respond to different keepers, suggesting that a special dyad is formed with a specific caregiver, which influences the animals' behavioral response. In this sense, high latencies to respond could represent fearfulness toward unfamiliar humans. Keeper familiarity was studied in bonobos (*Pan paniscus*), revealing that familiarity elicits more sociosexual interactions as a way to redirect excitement, as familiar keepers are associated with rewards (food) (Caselli et al 2023).

For the same species of black rhino (*D. bicornis michaeli* and *minor*), cheetahs (*Acinonyx jubatus*), and maned wolf (*Chrysocyon brachyurus*), Carlstead (2009) evaluated animal responses to keepers such as affinity, fear, sociability or curiosity. This study concluded that the time that keepers spend with animals and even their posture and behavior affect their response. For example, maned wolves and cheetahs tended to show aggression or apprehension when keepers performed rapid movements or unexpected noises. Additionally, when comparing the fGCM levels from previous reports to correlate the animal's behavior with a physiological response (Carlstead and Brown 2005), it was found that rhinos who had a fear reaction toward keepers had higher fGCM (r=0.73), a similar outcome in cheetahs cataloged as tense and fearful (r=0.61) (Carlstead 2009).

The correlation between glucocorticoid release and behavioral parameters was also assessed for different species of rhinoceros by the same researchers. In black (*D. bicornis*) and white rhinoceros (*Ceratotherium simum*), Carlstead and Brown (2005) determined that white rhinos who had a friendly relationship with their keepers had lower corticoid levels, and those exhibiting stereotypic behaviors (e.g., pacing) had higher values. In black rhinos, a correlation between enclosures where visitors could see the animals on a greater perimeter and a higher mean fGCM (r=0.53) was reported, as was the association between the fGCM and average zoo mortality. Similarly, in African (*L. africana*) and Asian elephants (*E. maximus*), serum CORT levels, attitudes of keepers toward their job, elephant behavior, and keeper-elephant relationships were analyzed to determine the well-being of the pachyderms. In *Loxodonta* individuals, low serum CORT levels are related to friendly and affiliative interactions with conspecifics and visitors, while in *Elephas*, lower levels correspond to public interactions and consider the keeper a herd mate (Carlstead et al 2019).

When zoo animals recognize zookeepers as social companions, this motivates positive reactions toward other staff members and possibly toward visitors (Shepherdson and Carlstead 2020) as a result of habituation. This was suggested in a study performed by Fink et al. (2022) in three Borneans (*P. pygmaeus pygmaeus*) and Sumatran orangutans (*P. pygmaeus abelii*), in whom fGCM levels were higher when the individuals were transferred to a veterinary medical center (a range between 64.30 ± 55.05 and 277.44 ± 190.49 ng/g) but were not particularly affected by intrainstitutional transfer. The authors concluded that although CORT values changed, the adrenal response was not intensively marked due to the interaction with the staff, which might have habituated the animals to humans. Therefore, to assess HAR using animal-based parameters in wildlife under human care, it is important to consider individual responses where habituation and previous experiences with humans can modify the exhibited change (Free et al 2022), particularly when exposed to uncontrollable and unfamiliar stimuli such as visitors.

5. Human-animal relationships with visitants

5.1. Behavioral effects of the VAI

VAIs are common in zoological institutions worldwide. Nonetheless, the number of visitors, noise, and behavior can cause positive, negative, and neutral reactions from zoo-housed animals, potentially affecting their welfare (Learmonth et al 2021). For example, a visitor score was used to assess the impact of the VAI on ebony langurs (*Trachypithecus auratus*), considering the frequency of displacement activities, affiliative behaviors, and aggression. The authors found that a higher visitor impact score (more than six points) was associated with an increased frequency of displacement behaviors (e.g., yawning) (0.254 ± 0.080), aggressions (0.349 ± 0.109), and scratching (0.181 ± 0.013). The animals also spent more time sleeping, with mean visitor impacts above three. However, although such responses can be associated with stress and negative VAI scores, ebony langurs also exhibit more affiliative behaviors, which might be used as a coping response (Roth and Cords 2020). A similar positive response was reported in Easter black-and-white colobus monkeys (*Colobus guereza*), swamp monkeys (*Allenopitheus nigroviridis*), DeBrazza monkeys (*Cercopithecus neglectus*), Bolivian gray titi monkeys (*Callicebus donacophilus*), and crowned lemurs (*Eulemur coronatus*) (Cairo-Evans et al 2022). The study considered the distance of the animals from the visitors and studied whether crowd size influenced the behavior of the species. Data collected over periods of up to 32 months showed that the number of visitors was a predictor of primate distance from the exhibitor, meaning that as the crowd increased, the distance from the visitor glass decreased (Cairo-Evans et al 2022). These results showed that the evaluated species of primates did not retreat from the exhibitor regardless of the increased number of persons, suggesting that the VAI was not a particular stress factor. Both studies showed that visitors cause arousal to zoo-housed species. Nonetheless, the ambivalence of said results must consider the so-called "learned helplessness" an event where the animal cannot cope or appropriately react to an uncontrollable stimulus and cannot avoid it. This phenomenon can be observed as an increase in resting time when exposed to a high number of visitors, as observed in a chimpanzee (*P. troglodytes*) group, in whom resting might—or might not—represent a relaxed state (Duncan et al 2022). Therefore, the controversy about learned helplessness is a factor that requires further study.

The coronavirus disease 2019 (COVID-19) pandemic opened an opportunity to investigate the dynamics of VAI during the global closure of most zoological institutions (Frost et al 2022). It was reported that during the COVID-19 closure of zoos, positive impacts were observed in several orders of animals (e.g., Carnivora, primates, Anseriformes, and Artiodactyla), such as mating behaviors (7%) and looking relaxed (20%), while negative impacts were described as missing (36%), looking lonely (3%), bored (5%) or stressed (4%) (Hunton et al 2022). Specifically, a questionnaire by Hunton et al. (2022) of 40 keepers from different countries reported positive behavioral changes, such as increased foraging, social play, enclosure usage, relaxation, and fewer interactions with humans. In contrast, within the negative outcomes, increased aggression, vocalizations, stereotypies, and startling reactions were reported, together with a deterioration in training.

In a multispecies analysis including Chinese goral (*Naemorhedus griseus*), grevy's zebra (*Equus grevyi*), swamp wallaby (*Wallabia bicolor*), Rothschild's giraffe (*Giraffa camelopardis rothschildi*), nyala (*Tragelaphus angasii*), Chapman's zebra (*Equus quagga chapmani*), snow leopard (*Panthera uncia*), and Amur leopard (*Panthera pardus orientalis*), Williams et al. (2021a) studied their behavior in the first month and the subsequent month after reopening. A significant increase in vigilance frequency in nyala, giraffe, Chinese goral, and swamp wallabies was found, while the opposite reaction was reported in Chapman's zebra. Another trait that did not differ was enclosure usage, where Grevy's zebra was the only species that spent more time in areas closest to the public after reopening. According to these results, reopening did not cause a negative HAR (Miller et al 2021).

In primates, one of the most studied species regarding VAI, a study performed on bonobos (*P. paniscus*), chimpanzees (*P. troglodytes*), western lowland gorillas (*G. gorilla gorilla*), and baboons (*Papio Anubis*) assessed the effect of the closure period due to COVID-19 and the influence of visitors on the behavioral response when reopening. Bonobos and gorillas spent less time alone when the zoo reopened (−0.312 ± 0.11 and −0.46 ± 0.20 number of observations, respectively); additionally, chimpanzees spent more time feeding (+0.25 ± 0.10) and interacting with enrichment methods (+1.58 ± 0.74). Gorillas also spent less time in enclosure zones near visitors, and baboons interacted more with humans and vehicles (whether ranger or visitor's vehicle) (+1.824 ± 0.201) (Williams et al 2022). These results show the potential negative stimulus of visitors due to the restlessness observed in nonhuman primates, an element that also affects enclosure use. These are factors that need to be considered when designing the enclosure of animals; for example, it can be sustainable for visitors to watch the animals but also to provide reassurance to the species when large visitors might be temporary stressors (Wark et al 2023).

While negative HAIs might be commonly reported between visitors and zoo-housed species, Williams et al. (2021b) reported positive and neutral responses from meerkats (*Suricata suricatta*) and African penguins (*Spheniscus demersus*) during the closure and reopening of zoos during the pandemic. While penguins did not significantly change during or after closure (representing a neutral interaction), the frequency of observation of positive social interactions in meerks increased when the facility was open (between 0.06 ± 0.24 and 2.39 ± 2.07), as did vigilance (4.92 ± 1.31 vs. 2.17 ±. 2.64). Other significant differences during the closure periods were greater environmental use (2.2 ± 1.4 vs. 1.7 ± 1.3) and greater enclosure usage (0.53 ± 0.23 vs. 0.19 ± 0.09). This reaction, although not studied, might be related to the animals looking out for humans during the closure or to animals retreating from the public (Hunton et al 2022).

The before-and-after pandemic period also permitted evaluation of the effect that visitors have on the presentation of stereotypies in wildlife under human care. Stereotypies (defined as repetitive behaviors without apparent function) are often used as behavioral markers of compromised welfare due to fear or stress (Sherwen and Hemsworth 2019). Although several factors influence the presentation of these abnormal behaviors, this is a relevant aspect of zoos due to social pressure and because the presentation of these behaviors differs according to the species (e.g., primates engage in regurgitation, self-scratching or self-mutilation behaviors; carnivores, in pacing; and ungulates, in licking and tongue flicking) (Sherwen and Hemsworth 2019; Taberer et al 2023).

A study by Masman et al. (2022) compared the frequency of regurgitation and reingestion (R/R) in gorillas (*G. gorilla gorilla*) before (2019) and during the pandemic closure of zoos (2020). Stereotypies were twice as frequent when visitors were present (almost 10%) in three of the four animals but did not change in one. However, for a female individual, the activity budget destined for R/R increased from 15.31% with visitors to 23.40% during closure. The authors also reported that gorillas autogroomed more frequently with visitors, and an adult male individual engaged in plucking more often. This is relevant because self-directed displacement behaviors such as autogrooming, scratching, or yawning have been associated with stress in primates (Taberer et al 2023). For the same species, without visitors, 83.33% of gorillas decreased foraging and increased their inactivity levels. These observations show the complexity of behavioral-based assessments of HAR and welfare because reactions can differ between individuals from the same species, and other traits need to be considered, including physiological markers.

5.2. Health effects

Endocrine assessment through fGCM quantification is the most common method for evaluating VAI, as reported for male blackbucks (*Antelope cervicapra L.*) to determine the effect of visitors, along with behavioral responses. It was found that days with a high and extremely high number of visitors (between 2632-4677 and 4851-36886, respectively) were significantly correlated with higher levels of CORT (113.51 ± 3.70 and 137.30 ± 5.88 ng/g, respectively). Moreover, these changes were also related to behavioral alterations in moving, resting, reproductive, social, and aggressive states (Rajagopal et al 2011). Among the samba deer (*Cervus unicolor*), adult males had higher CORT concentrations than females did (276 ± 52.74 vs. 181.56 ± 25.87 ng/g), and higher fGCMs were correlated with a greater number of visitors (r= 0.482) and greater frequency of visitors (r=0.398) (Gholib et al 2021).

During the COVID-19 pandemic, several analyses using the fGCM were also published. Fink et al. (2021) performed studies on cheetahs (*Acinonyx jubatus*) and giraffes (*G. camelopardis reticulata* and *G. tippelskirchi*) to determine the effect of COVID-19 closures on the endocrine response. In both species, there was a significant increase in fGCM. In giraffes, the increase in the fGCM concentration was 22.7 ng/g. However, this increase was not solely related to a visitor effect but also to confounding variables such as veterinary care and medical procedures performed during the study. Moreover, the physiological evaluation was corroborated by behavioral changes in which giraffes were more vigilant when the zoo was closed (possibly due to habituation to human sounds) and in which the cheetahs increased the amount of time not visible without visitors (Fink et al 2021). In contrast, the fGCMs of bonobos (*P. paniscus*), chimpanzees (*P. troglodytes*), western lowland gorillas (*G. gorilla gorilla*), and baboons (*Papio Anubis*) did not significantly change due to VAI in the reopening of zoo and safari parks (Williams et al 2022).

Currently, safe parks or nature-based tourism involving wild species under human care are proposed as alternatives to promote positive HAR. A neutral HAR was reported in a study with free-roaming giraffes (*G. camelopardis*), in which the fGCM increased (approximately up to 1.0 µg/g DW) when an observer was present but decreased when the animals became habituated to the human presence. The same response was observed for behavioral patterns such as walking further when humans were present (44.1%) and increased vigilance (Scheijen et al 2021). Nature-based tourism is worth discussing because some studies have assessed the effect of VAI and habituation. In orangutans (*P. pygmaeus morio*) situated in a wildlife sanctuary, Muehlenbein et al. (2012) determined the fGCM concentration in habituated and nonhabituated animals. The results showed that fGCM levels were lower in habituated individuals (1272-1933 *and* 1821-2188 ng/g, respectively), which may suggest that orangutans do not experience chronic stress and that low levels of predictable disturbance are key to avoiding strong physiological and stress responses. These results suggest that one approach to avoid stress responses and negative KAR and VAI in zoo animals is through habituation to their environment and human presence. In this sense, strategies such as environmental enrichment—particularly social enrichment—and positive reinforcement training are applied worldwide to maintain animal welfare (Fernandez and Martin 2021).

6. Proposed strategies to improve human-animal relationships in wild species under human care

6.1. Environmental enrichment (EE)

Environmental enrichment (EE) is a husbandry tool in which the provision of social, nutritional, physical, sensory, and cognitive stimuli encourages the expression of natural and species-specific behaviors in captive species (Riggio et al 2019; Riley and Rose 2020). Since biological needs differ between animals, EEs must be suitable and objectively designed for the species (Kiranaputri et al 2021). Several studies have reported the benefits of EEs in zoos, such as reducing stereotypies in walruses (*Odobenus rosmarus*) (Fernandez and Timberlake 2019) and promoting foraging and appetitive behaviors in polar bears (*Ursus maritimus*) (Fernandez 2021).

Public feeding can be considered a type of social and nutritional enrichment, as suggested by Fernández et al. (2021) for three zoo-housed Asian elephants (*E. maximus*). The authors evaluated the behaviors of the elephants before, during, and after public feeding and during nonpublic feeding days. When comparing the average activity during nonpublic feeding and public feeding, the elephants increased social interactions (>90% with their keepers) and decreased the frequency of stereotypies (rocking and pacing) in two of the elephants (the highest change was from approximately 33% to 20%). After the session, the animals engaged more in foraging (+25 from baseline) and exhibited less inactivity (-15 from baseline). Likewise, feeding programmes in Masai giraffes (*G. tippelskirchi*) and plains zebra (*E. quagga*) did not result in behavioral alterations, regardless of the number of visitors. There was no significant increase in stereotypies (pacing and licking); however, during the prefeeding period, 8.33% of the giraffes were stereotyped, 9.65% were stereotyped, and 4.4% were stereotyped on nonfeeding days (Koopman et al 2023). The authors concluded that food EE enhances positive HAR. However, individual differences were present, and this is an essential trait that needs to be considered when evaluating HAR and behavior. The same outcome was observed in European wolves (*Canis lupus lupus*) by Riggio et al. (2019). Neither activity nor inactivity behaviors differed during the feeding sessions. Interestingly, the type of enrichment and the way the food is provided influenced stereotyped (pacing and jumping against the fence) presentation in wolves. Providing novel objects resulted in lower stereotypy rates (0 observations) in 50% of the animals; hiding food increased social play and affiliative interactions in one subject, while artificial feeding objects decreased agonistic and aggressive interactions in 50% of the animals. Additionally, the increased interest of visitors during the enrichment sessions showed that public feeding can sustain both animal welfare and the role of zoos as an institution open to the public to inspire and promote interest in nature and wildlife conservation by helping visitors participate in these events.

In addition to feeding animals, other interactions, such as touching, walking, and riding, are suggested as EEs for wild species under human care. This phenomenon was evaluated in African elephants (*L. africana*) by Manning et al. (2022), who evaluated the frequency of self-directed behaviors in a tourist attraction involving a human-animal close-contact experience. We also used the fGCM to assess stress and anxiety in these animals. No differences in fGCM were found for the elephants, but self-direct behaviors increased during walks (coef=0.82) or rides (coef=0.63), while touch had the opposite effect (coef=-0.23). According to this study, walking and riding were potential stressors, while touching animals gave them the option to not participate in the event, an element linked to positive HAR and good welfare (Mason et al 2007; Fernandez 2022). However, Hutchinson (2005) mentioned that, according to the species, providing multiple choices to animals could also be deleterious, a response that requires further research.

Modifying or changing the enclosure is another type of EE where the main goal is to provide more naturalistic exhibits to wild species, but this approach can also incite positive VAI. Behringer et al. (2022) evaluated the impact of moving bonobos (*P. paniscus*), gorillas (*G. gorilla gorilla*), and orangutans (*P. abelii*) to a new enclosure by assessing salivary CORT concentrations. They found a greater salivary CORT intercept in the new enclosure, indicating that CORT levels increased. This might be indicative of a stress response; thus, when adopting enrichment, it is important to consider whether the species (and even the individual) can cope with new situations. Lion-tailed macaques (*Macaca silenus*) that moved to a new larger environment but were closer to visitors were used. This resulted in an increase in out-of-sight behavior (due to exploratory behavior in the new enclosure) and less time spent engaging in self-directed behaviors (scratching and autogrooming) (from 0 to 1%), representing a decrease in displacement behaviors associated with stress, frustration, and anxiety (Hosey and Melfi 2020). This approach is relevant because one of the challenges of current zoos is to maintain the visibility of animals to the public without compromising their welfare, but a decrease in adverse reactions has been observed when the animals are housed in naturalistic enclosures. For example, animals provided with new enclosures tend to spend less time inactive because they explore or forage and use larger extensions of the exhibit, as shown in orangutans (*P. pygmaeus*) (Dalimunthe et al 2021) and elephants (Glaeser et al 2021).

6.2. Positive reinforcement training (PRT)

Conditioning training is a tool for promoting the welfare of zoo-housed species. Training facilitates daily routines, medical examinations (e.g., minimally invasive drug administration and blood sampling, ultrasound scans), and husbandry procedures and helps individuals form bonds with keepers (Melfi 2013). Positive reinforcement training (PRT) is a type of conditioning learning in which animals voluntarily cooperate and control access to rewards after performing a desired behavior (Hambrecht et al 2021; Nekaris et al 2022).

PRT is commonly used; therefore, animals can voluntarily permit stress-free medical sampling, improving the HAR between the animal and the veterinarian, an interaction that is known to be stressful in domestic and wildlife settings. Examples are husbandry practices when animals are trained to voluntarily enter crates for blood draws and other medical procedures (e.g., radiography, hoof care) using reward-based methods in a nyala (*Tragelaphus angasi*) bongo (*Tragelaphus eurycerus*), giraffes (*G. camelopardis reticulata*), chimpanzees (*P. troglodytes*), and mangabey (*Cercocebus atys*), among others (Fernandez and Martin 2023). Similarly, female African lions (*P. leo*) have been trained on blood sampling and vaginal swabs without causing stress-related behavioral consequences (Callealta et al 2020). EE has also led to the development of the Great Ape Heart Project to establish, promote, and facilitate echocardiographic assessment since CVD is one of the main causes of mortality in zoo-housed primates (Boyd et al 2020).

PRT promotes species-specific behaviors that might help decrease abnormal or stereotypic behaviors (Leeds et al 2020). A study of Sumatran tigers (*Panthera tigris sumatrae*) applied the PRT as a social enrichment tool to reduce the frequency of stereotypical behaviors (pacing) and evaluate the stress response to blood sampling using the N/L ratio. All N/L ratios of the four tigers were significantly reduced with PRT (from an overall average baseline value of 21.25% to a postenrichment of 11.75%) (Kiranaputri et al 2021). Regarding stereotypic behavior, at baseline, all animals exhibited low stereotypic pacing (<33.33%), and no correlation was found between the N/L ratio and stereotypies. Similarly, Leeds et al. (2020) evaluated the effect of PRT on the endocrine response of lowland gorillas (*G. gorilla gorilla*) by measuring salivary CORT and oxytocin (OXT) levels. Although OXT did not change after PRT, CORT decreased (from 3.68 ± 0.4 ng/ml before PRT to 2.08 ± 0.2 ng/ml 30 min after PRT). Salivary CORT levels were used to assess the reaction of PRT in African elephants (*L. africana*) and to assess exposure to a novel object. When comparing the values before and up to 60 min after training or EE, the authors found a reduced salivary CORT concentration after PRT (23% lower at 15 min before PRT); the opposite reaction was observed when participants were exposed to the novel object (10% higher at 30 min postexposure) (Hambrecht et al 2021).

Other authors have mentioned that training in public displays is a method in which the bond between the trainer and keeper is improved and serves as an educational program where visitors can be entertained and learn about the biological or behavioral traits of the species, as observed in giraffe feeding experiences and small primate encounters (Whitehouse-Tedd et al 2020). Furthermore, in Abyssinian colobus monkeys (*Colobus guereza*), PRT increased KAR without negatively affecting the behavioral repertoire (resting and feeding) or daily activity budget. In contrast, the VAI was reduced, but this might be the result of interactions with keepers that allowed enough social retribution (Melfi and Thomas 2005).

As mentioned by Melfi (2013), although PRT can be considered an enrichment if it provides the animals with the opportunity to learn (cognitive enrichment) and might have the same goal as EE, it cannot substitute for EE, and adopting both strategies is suggested as an adequate approach to promote KAR, VAI, and animal welfare.

7. Final considerations

The HAR is part of the daily routine for zoo-housed animals, whether with their caregivers or visitors. These interactions can be affected by several keeper-, visitor-, and animal-related factors. For example, maintainers' experience, positive attitude, and knowledge about the species, as well as the time spent with the animals, facilitate HAR and reduce management-derived stress responses. Regarding visitors, direct and indirect contact experiences can have both negative and positive outcomes. A high number of visitors is mostly associated with an increase in displacement behaviors and vigilance. However, feeding programs with close VAI do not affect the behavioral repertoire.

The inconsistency of the reported zoo-housed animal reactions to humans is due to interindividual differences depending on the species, age, sex, familiarity with humans, and past experience. Therefore, promoting positive HARs in wild animals under human care is essential; EEs and PRTs are strategies that can aid in establishing beneficial relationships in animals. Nonetheless, when evaluating the effects of HAR on animal welfare and health, individual traits and physiological and behavioral responses must be considered when determining the emotional valence of HAR in zoo-housed species.

Ethical considerations

Not applicable.

Conflict of Interest

The authors declare that there is no conflict of interest with this work.

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