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Abnormal Behaviors in Captive Wildlife: To Keep or Not to Keep?

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ABSTRACT

Wildlife in captivity serves several purposes, including research, conservation, agriculture, and tourism. Many zoos and wildlife parks are driven towards conservation roles as they help prevent endangered wildlife from becoming extinct. However, a captive environment is often not the best manifestation of the animal's natural habitat, thus hindering them from performing natural behavior as they would in the wild. This imposes stress on the captive animals, leading to the display of abnormal behaviors, such as stereotypic behaviors, which are repetitive, invariant, and functionless behaviors. Stereotypic behaviors have been observed in many captive animals, such as pacing in tigers and bears, swaying and bobbing in elephants, over-grooming, self-mutilating, coprophilia, and coprophagia among captive primates, as well as fur and/or feather plucking in primates and birds. This article explores the abnormal behaviors of captive animals in response to their environment and highlights the critical importance of enrichment and naturalistic habitat design. Creating environments encouraging species-specific behaviors can significantly improve animal welfare, enhance conservation outcomes, and educate the public about wildlife conservation. Improved welfare practices not only support animal well-being but also strengthen public engagement and advocacy for conservation initiatives, ultimately aiding in protecting endangered species.

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INTRODUCTION

The suboptimal welfare of captive animals poses serious concerns that warrant effective interventions to improve their well-being. Beyond ethical considerations, this issue is pivotal in understanding the evolutionary development of animal behaviors [1] and its implications for conservation efforts. Observing unnatural behaviors exhibited by animals in zoos and wildlife parks often evoke a sense of unease, as signs of lethargy, inactivity, and stereotypic behaviors, such as pacing, swaying, or object-licking, are indicative of compromised welfare [2-5]. These behaviors are more than symptoms of psychological distress; they also reflect an animal's inability to adapt to specific environmental stimuli [6], posing significant challenges to conservation outcomes and raising important questions about captive wildlife's welfare and psychological well-being. Zoos and conservation centers are primarily established to conserve endangered species by captive breeding [7] and enhance research on animal behavior and ecology while also educating the public about the critical roles of wildlife in sustaining ecosystems [8-10], ultimately contributing to biodiversity preservation efforts [11].

However, when animals experience chronic stress in captivity [1], it can lead to a cascade of adverse effects, including impaired reproductive success, increased susceptibility to diseases, display of stereotypic behaviors [12], increased cortisol levels [10], all of which threaten long-term species survival [13]. A list of evidence points out the impaired well-being of captive wild animals, which indicates their needs are not being satisfied [14]. For example, herbivores, such as giraffes, are short-lived in zoos compared to when they are conserved in their natural habitat due to the lack of nutritional value and low energy in their food supply, indicating insufficiency in their diets [15]. Moreover, many giraffes in captivity displayed stereotypic behaviors such as object-licking [16, 17]. Similarly, stereotypic behaviors are widespread among other herbivores, including captive elephants [18-20] and carnivores such as tigers and leopards [10, 21, 22]. Addressing these welfare concerns of captive wildlife is not only critical for improving the quality of life for individual captive animals. However, it is also instrumental in achieving the overarching goals of conservation programs. Understanding the underlying factors and consequences of abnormal behaviors can inform the development of evidence-based strategies to mitigate stress, enhance reproductive outcomes, and support species' survival. Furthermore, captive wildlife displaying maladaptive behaviors may face challenges upon reintroduction to the wild. This article explores the types of abnormal behaviors displayed by captive wildlife, their relation to environmental stressors in captivity, and the measures required to minimize the occurrence of these behaviors and improve conservation outcomes.

Animal behaviours in captive wildlife

Natural behavior is displayed in environments that are pleasant for the animals and support their biological functioning [23]. Examples of natural behaviors common in wildlife are foraging and exploring habitat, as observed in many species, including sun bears [24, 25]. Wild orangutans also invest almost half of their time foraging and feeding [26] and prefer to stay in high spots throughout the day and night [27]. Conversely, Macaques are often observed to perform locomotor, investigative, and social activities in the wild [28]. Another example is free-ranging tigers that typically live in solitary and often patrol their wide home ranges or territories [29-33]. They are the apex predators in the wild and are great hunters. They normally hunt at night and occasionally during the day [30].

In captive environments, however, natural behaviors are commonly substituted with abnormal behaviors, including stereotypic behaviors such as pacing [34]. Abnormal behaviors can be defined as atypical responses that are not typically observed in the wild, displayed by animals exposed to specific stimuli and conditions they are unable to cope with [14], which are frequently interpreted as a form of coping mechanism that organisms utilize in response to stressors [35]. Captivity has been shown to induce anomalies in behavioral patterns across various species [36], including wildlife [37, 38]. This scenario poses significant concerns, particularly for threatened species, as it could adversely affect reproductive success, physiological health, and overall life span [39-41]. Behavior is a practical and widely utilized stress indicator in zoological research, as it can be systematically measured. This allows for an accurate assessment of animals' responses to environmental alterations, thereby providing insights into their well-being about environmental changes [42]. The inability of animals in zoos to exhibit normal behavior is often a result of environmental factors such as unfavorable weather conditions, unpleasant substrates, unnatural lighting, exposure to loud noises, and disturbing odors [40]. Barren settings, spatial limitations, restricted locomotion, lack of retreat area, inescapable proximity with humans, restricted contact with other species, lack of feeding variety and chances, social housing, and other limitations in behaviors are some of the stressors present in captivity [4, 43]. The effects of stressors depend significantly on how an individual perceives and responds to the stress agents [44].

Warwick et al. (2013) [45] stated that animals living in a confined setting or artificial ecosystem encounter numerous stressors that deviate from those typically experienced in their natural habitats. In most cases, animals housed in confinement with limited space have a high probability of developing stereotypic behaviors [4, 46], as the limited availability of space hinders the potential for environmental enrichment [47]. The inadequate space offered by the enclosures restricts animals from eliciting their normal species-specific behaviors, such as foraging and exploring their environment [4, 24, 25]. In addition, smaller enclosures are also associated with aggressiveness [48] and stereotypical pacing in tigers [10, 32, 49, 50]. In addition to limited space within enclosures, a lack of environmental stimulation can develop stereotypic behaviors [47]. In barren enclosures, animals typically respond to the lack of stimulation by either (1) decreasing their exploratory behaviors or (2) seeking to fulfill their exploratory needs through stereotypic behaviors [4], as can be seen in bears [24, 40].

Furthermore, enclosure type, high visitor density, and humidity also contribute to the development of abnormal behaviors. A study conducted by Arumugam et al. (2018) [51] highlighted the significant influence of enclosure type, humidity, and visitor density on the behavior of Malayan tapirs (*Tapirus indicus*) in captivity. Their findings indicate that tapirs housed in semi-natural environments exhibit a higher feeding frequency than those housed in artificial environments.

Introduction to stereotypic behaviors

Numerous studies across various animal species indicate that reproductive success and survival rates are higher in captivity than in their wild counterparts [52, 53]. However, when wildlife is placed in environments that significantly deviate from their natural habitats, they become increasingly vulnerable to developing stereotypic behaviors [54]. For instance, inadequate housing conditions, such as the absence of perches and hiding places for captive birds, primarily contribute to the manifestation of stereotypic behaviors [55]. Stereotypic behaviors are conclusively described as behaviors that are repetitious, invariant, and without clear functions, such as pacing, head bobbing, fur/feather plucking, and over-grooming [54, 56, 57], and are often indicative of psychological distress [58]. These behaviors are typically associated with stress experienced by animals in captivity [59] and are thought to arise from various stresses caused by boredom, physical constraint, fright, agitation, and frustration [50, 60-62]. Such frustration typically stems from the animals' inability to resolve persistent problems in captivity or perform natural species-specific behaviors [54]. For example, captive European starlings often exhibit stereotypic somersaulting [63], attributed to many repetitive, failed attempts to escape [64].

In this context, stereotypic behaviors are considered psychological behaviors synonymous with human psychological conditions such as anxiety, depression, and obsessive-compulsive disorder (OCD) [65]. In the early stages, such behaviors may serve as coping mechanisms to help animals adapt to environmental challenges. However, lacking opportunities to engage in diverse natural behaviors can lead to significant neurobiological changes, potentially impairing brain function and altering neural connections, physiology, and anatomy. Importantly, these neuroanatomical are often considered as a consequence rather than the root cause of the behaviors [66]. Furthermore, the manifestation of stereotypic behaviors has been extensively investigated concerning several factors, including personality traits [67], individual variability [68], sex-specific susceptibility [69], and genetic dispositions [70].

Stereotypic behaviors are widespread across taxa in captivity [3, 37, 71]. Primates were observed to display behaviors that are equivalent to certain depressive patterns observed in humans [72, 73]. Birkett and Newton-Fisher (2011) [36] reported that all 40 chimpanzees living in six accredited zoos displayed stereotypic behaviors, suggesting mental dysfunction akin to mental illness in humans. In addition to prosimians, giant pandas [37, 71, 74] and red pandas [75] in captivity were also observed to exhibit stereotypic behaviors that illustrate stressful conditions or poor well-being. Research also highlights differences in behaviors based on housing conditions. For example, fully captive omnivorous sun bears displayed significantly higher levels of stereotypic behaviors than those housed in semi-captivity (i.e., they were allowed to the forest during the day but housed in enclosures at night), likely due to multiple factors such as enclosure size and environmental complexity [76]. Captive wildlife exhibits diverse stereotypic behaviors, reflecting their responses to environmental stressors. The following sections explore common forms of stereotypies observed in captivity, including pacing, head tossing/bobbing/body swaying, excessive grooming, coprophagia, fur and/or feather plucking, self-mutilating, object gnawing and/or licking, genital stimulation, urophagia, investigative behaviors, and fearful behaviors, passive behaviors and aggression.

Types of stereotypic behaviors

Pacing

Pacing or circling is one of the most common stereotypic behaviors in captive wildlife. It is characterized by repetitive walking along the same path with no obvious objective [3, 32, 77] and is often an indicator of stress [78]. For example, horses often exhibit stereotypic circling within their stalls, even during feeding, showing a lack of interest in their surroundings [4]. In tigers, pacing is typically identified as walking in a figure-eight pattern with more than two rotations [56]. Among chimpanzees, the pacing is described as a quadrupedal locomotion along a repeated route in a conformed manner with no obvious goals [36]. The prevalence of pacing behavior has been widely documented across taxa. Carnivorous animals in captivity, such as tigers, spend much time pacing back and forth within their enclosure [10, 21, 22, 28, 56, 79]. Similarly, stereotypic pacing has been reported in various wildlife species, including leopards, bears, giraffes, and even sloths. Environmental stimuli, such as enclosure design, feeding routines, or human activities, often trigger such behavior. For instance, Mallapur and Chellam (2002) [80] reported that stereotypic behaviors in captive leopards increased in correspondence to the zookeepers' activities and during longer feeding periods. It was observed that the leopards paced significantly more when the zookeepers were cleaning the off-exhibit enclosures. Similar behaviors were observed during feeding time, in which they were seen to be agitated and restless. The leopards were also found to significantly increase their stereotypical pacing during high numbers of visitors, especially during festive seasons. Visitors can be stimulating for the animals, but constant exposure to the high density of visitors can be traumatizing [54].

Environmental stressors, such as limited control over the environment [81], restricted space, social isolation [16], unmet intrinsic needs [14], and inability to perform species-specific behaviors [82], exacerbate stereotypic pacing. For territorial species such as tigers, who naturally patrol their extensive wild home ranges [50, 83, 84], spatial constraints in captivity prevent them from engaging in such territorial patrolling [32, 50]. Furthermore, while wild tigers are skilled hunters, the fixed feeding schedules typical of captive settings limit opportunities for foraging behaviors, such as hunting prey. This restriction, coupled with anticipatory behavior around feeding times, often contributes to the development of pacing behavior [50]. Similar patterns have been observed in other carnivores, such as leopards [10, 85] and lions [86]. In addition, herbivores, such as giraffes, exhibit stereotypic behaviors in the form of repetitive pacing [16, 17], potentially due to spatial constraints. Other herbivores, including captive sloths, are also not excluded from displaying pacing [87].

Tailored strategies, including enrichment and enclosure modifications, have shown promise in reducing stereotypic behaviors. Pitsko [47] demonstrated that tigers kept in enclosures designed to mimic their natural habitat with the provision of natural substrates, vegetation, and shaded areas exhibited reduced pacing behavior and increased exploration. Interestingly, there was no incidence of stereotypic behaviors by two tigers that were kept in bigger enclosures throughout the observation. Natural substrates such as grass or hay beddings, leaves and grass, and wood chips are recommended to encourage typical species-specific behaviors in animals in captivity [88]. The captive tigers invested 90% of their time in well-shaded areas, indicating the necessity of having large, shaded areas, particularly on sunny days. For captive felids, artificial substrates that do not reflect naturally occurring substrates in the environment, such as concrete, not only increase stereotypic pacing [89] but can also cause physical injuries to the legs and throbbing footpads [88]. Such findings extend to other species. For example, a study comparing fully captive sun bears with semi-captive sun bears found that the fully captive bears spent significantly more time pacing [76]. The stereotypical pacing exhibited by the captive bears aligns with findings that associate pacing with animal stress, particularly in bears [38, 90]. The bears also paced significantly in the evening in anticipation of food, as it was routinely provided to them during that period [76]. Recognizing such taxa-specific differences is critical for developing strategies to improve welfare, such as enrichment that meets species-specific needs [91].

Head tossing, bobbing, and body swaying

Tossing or bobbing of the head is a circular or up-and-down motion performed without clear functions in a repetitive manner, classifying it as a type of stereotypic behavior [28, 92, 93]. This behavior is particularly prevalent in primates. For instance, zoo chimpanzees have reportedly exhibited repetitive head bobbing [36], as have captive-born macaques, frequently repeatedly moving their heads up and down [28]. Beyond primates, head bobbing has also been documented in elephants [35]. On the other hand, Swaying involves repetitive side-to-side movements of the head and body, typically performed at least three consecutive times [5, 46, 94] or by transferring weight rhythmically from front to rear and back again [46, 95]. Swaying is common among elephants [5, 19, 20] and has also been observed in cynomolgus monkeys [28]. Weaving, a related behavior characterized by head-swinging combined with shifting weight from one foot to the other without forward movement, is frequently observed in horses [4]. Bettinger et al. (1997) [96] suggested that head-swaying in the largest mammals, such as elephants, is a coping mechanism to soothe themselves. Maternal deprivation has been identified as a potential contributing factor to the development of these stereotypic behaviors. For example, captive elephant calves separated from their mothers after weaning are more likely to exhibit head bobbing or swaying, highlighting the role of early social and environmental conditions in the emergence of these behaviors [35]. This highlights the critical role of appropriate maternal care and enriched environments in mitigating the development of stereotypies in captivity.

Excessive grooming

Grooming or preening in some taxa, such as birds, fulfills both physiological and social functions in various species and is instrumental for survival and adaptation [97, 98] and ectoparasite removal [99]. However, in the presence of environmental stressors, grooming behavior is often displaced, resulting in the development of pathological excessive grooming [100-102]. Over-grooming or excessive grooming is characterized by repetitive grooming focused on specific body parts, apparently without any clear objective or intention. This behavior may also involve using objects such as sticks or other tools to lightly drag across body surfaces in a non-focused manner [36]. Over-grooming is considered a stress-coping behavior [103] and has been documented across taxa, particularly primates. For instance, captive chimpanzees often exhibit stereotypic over-grooming [36], while captive macaques lick their tails repetitively and various body parts, suggesting analogous behavioral patterns in these primates [28]. These behaviors may arise from the inability to engage in species-typical social grooming, such as allo-grooming among conspecifics [104].

Carnivores, including captive jaguars, have also been observed to display over-grooming behavior [105]. Potential underlying causes of over-grooming include chronic itching, leading the animals to over-groom, or even self-mutilating to alleviate discomfort [106]. Over-grooming may also result in hair loss, impairing thermoregulation and further exacerbating the animals' physiological stress [107].

Coprophagy

Coprophagy, the deliberate act of eating feces, involves animals ingesting their feces or that of another animal [108]. This behavior is often attributed to stress, boredom, and compromised welfare [109]. It has been observed across various taxa, including horses, pigs, koalas, and birds [110]. Among primates, chimpanzees have been documented engaging in coprophagy, often picking through their excretions and consuming the remnants of food and seeds found in their feces [111]. A study examining chimpanzees across six zoos identified coprophagy as one of the most prevalent stereotypic behaviors observed [36], a finding supported by additional research [108, 112]. Interestingly, infant chimpanzees were found to mimic this behavior after observing their mothers, suggesting that coprophagy can be a socially learned behavior despite its classification as a stereotype [108, 109, 112]. A similar pattern has been observed in koalas, where their infants consume maternal feces to acquire microbial strains necessary for digesting eucalyptus leaves [113]. Coprophagy is also reported in avian species, particularly among precocial birds such as quails, turkeys, and ptarmigans [110, 114].

Fur or feather plucking

Fur or feather plucking, depending on the species' concern, is a stereotypical grooming behavior in which an animal self-inflicts itself by pulling out its fur, hair, or feathers for no obvious reason. Fur-plucking is a behavioral abnormality observed in various species, including felids [115] and primates such as the great apes [116]. Captive chimpanzees, for example, have been reported to pluck not only their body hair but also the hair of their conspecifics [36]. Among carnivores, fur-plucking has been documented in captive tigers, cougars, and lions, often resulting in fur loss and skin irritation [117, 118]. Feather-plucking is particularly prevalent among captive birds, such as parrots [100] and cockatoos, and is frequently associated with limited opportunities for naturalistic behaviors, including foraging, social interactions, and physical exercise [55].

Hand-rearing has also been implicated in developing stereotypic behaviors such as feather-plucking, as observed in hand-reared grey parrots [55]. When directed toward conspecifics, this behavior is called feather-pecking, which leads to loss of feathers, tissue injuries, and pain, signaling serious welfare concerns [119]. The resulting bald patches can attract further tissue pecking, escalating cannibalistic behavior that can be fatal [120]. Feather loss also compromises the birds' physical condition, resulting in prolonged discomfort [119]. Controlling feather-pecking is particularly challenging in large groups, as social learning promotes the spread of these behaviors, including cannibalism, throughout the flocks [121]. Feather damage caused by feather-pecking is often linked to fear and the pain of being pecked, as observed in confined hens [55].

Self-mutilating

Self-mutilating or self-harming behaviors, including self-hitting and self-biting, occur when animals intentionally inflict injury upon themselves. These actions may involve striking their bodies against surfaces using hands, paws, or limbs to strike themselves or biting their skin or appendages [36, 92]. Various factors, such as improper diet, social frustration, aggressive tendencies, and boredom, have been suggested as potential contributors to the development of these behaviors [122]. Self-mutilating has been documented across a wide range of taxa. For example, a captive king vulture exhibited severe self-inflicted injuries that became contaminated, exposing underlying bone [123]. Similarly, self-harming behaviors such as self-biting and head-banging are also prevalent in primates [124]. Japanese macaques and pig-tailed monkeys have been observed repetitively rushing into wired enclosures, leading to self-harm [122]. In a study of zoo-living chimpanzees, Birkett and Newton-Fisher (2011) [36] reported self-harming behavior, such as hitting themselves with their hands. Apart from that, captive sun bears have also demonstrated self-mutilating behaviors, including self-biting, hitting, and pinching repetitively without any purpose [76]. Tail-biting is another form of self-injury commonly observed in pigs [125] and is often linked to improper diet, gut discomfort, compromised health, and genetics [4]. Similarly, self-mutilation is prevalent among felids, manifesting as behaviors such as excessing, licking, biting, or scratching [126]. In equines, self-injurious behaviors include self-biting, kicking, and pushing against stall structures, often reflecting frustration or discomfort in captivity [4]. Collectively, these examples highlight that self-mutilation is not confined to a specific group of animals but is a widespread issue in captive settings, often indicative of underlying welfare concerns.

Objects gnawing or licking.

Oral stereotypic behaviors, such as bar biting, wall licking, and substrate gnawing, are commonly observed in captive animals. These repetitive actions involve using teeth to lick, gnaw, or chew on objects within their enclosures. Such behaviors have been documented across various species. For instance, in a study of 40 male macaques on a breeding farm, individuals housed in solitary conditions exhibited repetitive oral stereotypies, specifically bar gnawing and licking [28]. Similarly, captive giraffes frequently display pronounced substrate-licking behavior, including wall-licking [16, 17]. In pigs, oral stereotypies such as bar-biting and sham chewing are prevalent [127]. Bar-biting is often interpreted as an attempt to escape, whereas sham chewing is a displacement behavior that substitutes actual feeding [128]. A survey revealed that nearly 80% of giraffes and okapis displayed stereotypic behaviors, with substrate licking accounting for 72% of these observed behaviors, as stated by Lewis et al. [129]. In horses, oral stereotypies such as crib-biting, wood chewing, and wind sucking are particularly common. Crib biting involves biting into their cribs, fences, or other stall structures [4], and these stereotypies are typically associated with increased stomach acidity [4]. These behaviors emphasize the need for tailored interventions to address underlying causes, such as environmental stressors or physiological imbalances.

Genitals non-sexual stimulation

Genital stimulation refers to the repetitive act of an animal stimulating its genitalia through actions such as touching, patting, clinging, fondling, and/or rubbing it continuously, typically in a non-sexual context. These behaviors have been observed in multiple captive species. For instance, Camus et al. [28] reported that macaques kept in a breeding farm repeatedly clung to their genitalia and atypically stimulated neighboring conspecific's genitals. Similarly, captive chimpanzees have been documented to touch, pat, stroke, and fondle their genitalia repetitively in non-mating conditions [36].

Urophagia

Urophagia or urine consumption is a form of stereotypic behavior in which an animal ingests its urine or that of others, typically by licking. This abnormal behavior is prevalent in primates such as macaques, chimpanzees [130], and other species, including birds. For example, urophagia has been documented in chimpanzees across six different zoos [36].

Investigative behaviours

Investigative or attentive behaviors, including sniffing and observing surroundings, are often performed when an animal is curious about environmental stimuli. This stimuli-seeking or exploratory behavior is typical of animals to survive, especially in the wild. However, repetitively displaying it due to stressors present in captivity is considered an abnormality. For example, Arumugam et al. [51] in his study also reported that investigative behaviors displayed by the Malayan tapirs, such as sniffing, general alertness, or observing surroundings while standing in stationary, sitting, or lying down, were higher in artificial enclosures than the semi-natural ones. This is due to the possibility of the tapirs being kept in an artificial environment exposed to blaring sounds from activities such as renovation works, traffic, and zoo visitors.

Fearful behaviours

Fearful behaviors such as being vigilant, constantly alert, quivering, fleeing, or hiding from non-harmful variables often result from stressful, traumatic experiences. For instance, captive tapirs in Zoo Melaka were found to be vigilant and always watchful of their surroundings. They displayed fearful behaviors such as tensing, alert, and fleeing to hide when hearing the noises from visitors, which frequently led to them quivering [51]. These behaviors were also observed in a tiger kept at the National Wildlife Rescue Centre (NWRC). According to the zookeepers, the said tiger possessed fearful behaviors such as panting, tensing, alertness, and fleeing to hide under platforms every time it heard growls of other tigers as well as any noise from surrounding due to its experience of being contained next to sun bears, not near its conspecifics. Consequently, the poor tiger had difficulty coping with the presence of other tigers. This aligns with the findings of Mason and Latham [131] and Wickins-Drazilova [132], who suggested that stereotypies arising from specific past experiences may diverge from their original causes and can persist in later stages of an animal's life, even in circumstances where such stereotypic behaviors are less likely to manifest.

Passive behaviours

Being passive includes standing still (stationary), lying down, resting, and sleeping. For example, sun bears in fully captive environments were observed to be significantly more passive than those in semi-captive environments [76], as they spent more time resting and sleeping, mostly in the afternoon. Kamaruzaman et al. [133] also reported that giant pandas invest most of their time inactive, which is different from their counterparts in the wild due to the constant routine provision of food in zoos. This gives them plenty of time to rest and be inactive, whereas the wild giant pandas forage for food to survive. Research showed that male giant pandas preferably spend plenty of time feeding and moving while female giant pandas tend to rest more [134]. Giant pandas in Zoo Negara, Malaysia, preferred to invest their time being inactive in rocky and cool areas as it mirrors the natural habitat of giant pandas, which is rocky, lush terrain in China [133]. With many visitors, fewer locomotor behaviors were also observed in Malayan tapirs [51]. They swam, investigated less often, and became more passive as they rested more when the number of visitors peaked. They also spent much time submerged inside the pool to avoid visitors' disturbances, such as poking and pouring water onto them [51].

Aggression or agonistic behavior

Aggressive or agonistic behavior is a type of negative social interaction [135] that can trigger stress reactions [136]. Nelson [137] stated that aggressive behavior is elicited to inflict harm or distress on another animal. Limitations in mating partners, food resources, and territory contribute to the appearance of aggressive behaviors [136]. Aggressive interactions can be observed in mammals, such as in sun bears. Restriction in exhibiting their typical behaviors in captivity contributes to stressful conditions and discouragement, which cause them to become hostile, violent, and harmful to each other and, therefore, could be destructive to their welfare [76].

Another example is captive Dorcas gazelles. They demonstrated aggressive behaviors such as butting, hitting, thrusting, striking, and pushing each other with their forehead, horns, and other body parts with force, chasing, and fighting [136]. Aggressive behaviors such as pecking, standing offs in which individuals vocalize and swing their heads in the display, and chasing [138] were also observed in captive flamingos [139].

Ways to reduce abnormal behaviors and nurture natural behaviors

The ethical debate over keeping wildlife in captivity hinges on our ability to minimize the adverse implications of confinement, particularly the prevalence of stereotypic behaviors. Animal rights advocates contend that captivity inherently infringes upon animals' intrinsic values and freedom [140]. On the other hand, utilitarian conservationists justify captivity as a necessary means to safeguard species from extinction, foster public education, and facilitate research [141]. Reconciling these perspectives is essential to ensure ethical practices align with conservation goals while prioritizing animal welfare. Central to this discussion is the design of captive environments that prioritize the provision of naturalistic habitats, which encourage captive animals to behave naturally while mitigating abnormal behaviors. Environmental enrichment is a significant tool for promoting wildlife welfare by enhancing reproductive and behavioral health [142, 143]. Through the use of diverse strategies [144], such as the inclusion of natural substrates, foliage, water bodies (i.e., pools), hiding spots, climbing structures such as logs, platforms, ropes, and other environmental items, make captive conditions more favorable and conducive to promote active, exploratory and natural behaviors [145] for various species including felids and primates. For instance, Gomes et al. [146] demonstrated that increasing environmental enrichment was associated with reducing stereotypical behaviors in captive tigers, reaffirming the potential of well-managed captivity to nurture natural behaviors. One widely used approach is foraging enrichment, which involves introducing novel food items to captive animals [147] or increasing the complexity of accessing food [148]. In cheetahs, for instance, exposure to such enrichment led to a marked increase in exploratory behaviors and a notable reduction in pacing behaviors [149]. Olfactory enrichment has similarly been shown to reduce stereotypic behaviors [150-152] and to foster natural and territorial behaviors [153, 154], as evident in black-footed cats [155].

In the wild, free-ranging animals can choose their habitat based on the necessities they require, such as food sources, shelter, and protection, adapting their behaviors to suit their environments [156]. In contrast, captive animals are subjected to rigid conditions, including routine activities and fixed diets, limiting their natural responses and changing their behavioral patterns [157], leaving them with little to no control over their environment [158]. To address these limitations, zoos and institutions must optimize enclosure designs, incorporating larger, more complex spaces with sufficient features and proper management to nurture natural, species-specific behaviors such as scent-marking [159], locomotor repertoires [32, 160] and minimize the prevalence of stereotypies [32, 161]. Alternatives to traditional captivity, sanctuaries, and semi-captive environments provide more naturalistic habitats and prioritize animal welfare. Sanctuaries typically offer animals greater autonomy and access to environments that closely mimic their natural habitats, leading to reduced stress and a decline in abnormal behaviors [162]. Similarly, semi-captive environments integrate aspects of wild habitats with managed care, fostering improved welfare outcomes and encouraging the expression of natural behaviors while maintaining opportunities for conservation and education [163]. Evaluating these approaches offers insights into more ethical and effective captive wildlife management. Enriched environments encourage captive animals to utilize more naturalistic areas [164], and studies indicate that spatial constraints contribute to displaying stereotypic behaviors. For example, Breton and Barrot [50] identified an inverse relationship between enclosure size and pacing, aligning with the findings of Clubb and Mason [60]. Animals housed in bigger, more complex enclosures exhibited reduced stereotypic behaviors compared to those housed in smaller, barren spaces [158]. Tigers with access to larger, enriched environments displayed more inherent behaviors and experienced a reduction in stereotypies [32].

In addition to larger spaces, providing manipulable and consumable items has significantly elevated natural behaviors in captive animals, particularly primates such as orangutans, where such enrichment is associated with a marked reduction in passive and stereotypic behaviors [44]. Gippoliti [27] reported that wild orangutans invested their day and night by being in aerial environments, and this offers a great window for zoological institutions to install ropes and lofty platforms to nurture the development of arboreal activities, which are synonyms with primates like orangutans [165]. Social enrichment has also proven beneficial, particularly in felids, where housing animals with conspecifics or near them has been shown to reduce stress-related behaviors [166 - 168]. Furthermore, auditory enrichment, such as the playback of recorded lion roars, has been shown to stimulate natural behaviors, including increased live roaring and playful interactions among lions [169]. Similar effects have been observed in African birds, where auditory stimuli such as natural sounds enhanced activity levels [170], further emphasizing the potential of auditory enrichment to encourage naturalistic behaviors in captive animals.

Emerging digital tools, such as computers and tablets, offer innovative cognitive enrichment, providing challenges and diverse problem-solving opportunities for captive animals, particularly primates [171-174]. Advances in digital technology have enabled researchers to develop virtual environments where animals can interact with and exert control over their environment [174], offering sustained cognitive stimulation and mitigating the risk of rapid habituation often associated with traditional enrichment methods [171, 172, 175]. These tools can be tailored to accommodate various animals based on age, sex, social rank, and cognitive abilities [174]. Environmental enrichment devices (EEDs) have similarly demonstrated significant positive effects on animal behaviors and physiological and psychological advantages, as mentioned in Donald et al. [91]. For example, EEDs have been shown to reduce stereotypic pattern swimming and increase exploratory and foraging behaviors in ill harbor seal pups [176]. Tailored EEDs have also effectively reduced stereotypical behaviors in California sea lions and northern elephant seals in rehabilitation centers [91]. While genetic selection is a potential method for reducing stereotypies, it is rarely utilized in zoos despite its common application in agricultural and breeding settings [177]. This method, which avoids breeding individuals exhibiting stereotypic behaviors [38], is less favored in captivity due to the underlying environmental factors contributing to such behaviors. Genetic engineering, although potentially effective in addressing issues such as feather pecking [119], is not widely considered, as stereotypies typically stem from environmental deprivation and frustration.

To optimize enrichment, captive management and caretakers must consider species-specific needs and individual differences, including personality traits such as shyness or boldness, which influence how animals respond to enrichment [178]. These traits may manifest as variations in the intensity or expression of specific behaviors or as distinct behavioral patterns within similar contexts, ages, or timeframes [179]. Such behavioral differences often arise from the interaction of endocrine, neural, and immune processes, collectively called “psycho-neuroimmunology,” which influence and are influenced by behavior. These processes significantly shape personality development within the boundaries of an individual’s genetic predispositions [180]. When introducing enrichment, individual preferences, background history, and needs must also be considered [181]. For instance, while some captive macaques benefit from enrichment, others exhibit no significant changes in stereotypic behaviors [181]. Social enrichment may have little to no positive effects on species such as giraffes and okapi, which are solitary by nature [16]. Conversely, species such as horses have shown marked reductions in stereotypies when provided with more fibrous diets, special feeding devices, stalls, and social enrichment [4]. This finding underscores the importance of considering variation in species and individuals in responding to enrichment.

While enrichment strategies should address the species' general behavioral and physiological needs, tailoring these approaches to align with individual differences, including personality traits, history, and preferences, is crucial to optimize their effectiveness and mitigate stereotypic behaviors [91]. Enrichment strategies specific to carnivores such as tigers and lions, such as frozen blood cubes, food hung on climbing poles, feeding boxes, feeding poles, simulated prey, and buried meats, have been shown to foster feeding and hunting behaviors [77, 102, 117, 158, 182, 183]. These methods not only improve animal welfare but also enhance visitor experiences. Visitors prefer observing animals in naturalistic enclosures displaying various interactive and active behaviors [184], while stereotypic behaviors and a lack of natural behaviors can detract from the exhibit's appeal [185]. Transitioning enclosures to more complex and naturalistic designs benefits the well-being of animals [186, 187] and conservation efforts by providing a more enriching environment for the animals and a more engaging experience for the visitors [184]. Ultimately, addressing abnormal behaviors in captivity is not about negating the values of captivity itself but rather about improving it to align with animal welfare standards. With effective strategies, captivity can contribute positively to conservation, education, and research, ensuring the well-being of the animals while furthering broader conservation initiatives.

CONCLUSION

Wildlife in captivity plays an instrumental role in conservation, education, and public engagement. However, it inevitably raises welfare concerns, particularly regarding the development of abnormal behaviors, particularly stereotypies. These behaviors indicate poor welfare and challenge the ethical basis of keeping animals in captivity. The answer to “To keep or not to keep?” lies in the equilibrium between the benefits and challenges of captivity. Captivity can be justified if it significantly contributes to conservation, education, and research while upholding rigorous welfare standards. To ensure ethical captivity practices, zoos and institutions should adhere to clear guidelines, which include prioritizing enclosure designs that closely resemble wildlife natural habitats, implementing a variety of species-specific and individualized enrichment measures to minimize the occurrence of abnormal behaviors, and tailoring management practices to address animal needs and preferences. Captivity should not be viewed as a binary condition but as a continuum where consistent improvement in welfare practices and interventions can significantly impact. For example, bolstering conservation programs and fostering natural behaviors through innovative technologies that can elevate the quality of life for captive wildlife. Housing wildlife in captivity is not inherently detrimental when done responsibly and ethically. Institutions must actively address welfare concerns and continually advance conservation goals. By doing so, captivity can remain a viable solution for wildlife survival and public education and awareness, ensuring that captive wildlife serves as conservation ambassadors rather than confinement symbols. However, if these standards are neglected, the ethical justification for captivity diminishes. Looking ahead, further research is needed to evaluate the long-term effects of enrichment on animal welfare, particularly in reducing stereotypic behaviors and nurturing natural behaviors.

Additionally, exploring the role of genetics in susceptibility to stress could offer valuable insights into tailoring individualized management strategies for different species and individuals. These studies will refine existing practices and guide the development of more effective and ethical captivity models. A forward-thinking approach requires ongoing commitment and innovation, ensuring that captive wildlife thrives while inspiring global conservation efforts.

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AUTHOR'S CONTRIBUTION

Nurfarah Ain Limin conceptualized, drafted, wrote, and revised the article. Nurfatiha Najihah Fakhrul Hatta drafted and provided technical input. Nur Adilla Zaki provided technical input and contributed to the article's revision. Nur Nadiah Md Yusof conceptualized, supervised, and reviewed the article.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

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