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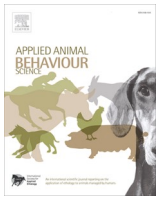

Review of depressive-like behaviours in some group-living mammals

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ABSTRACT

Thanks to animal models of depression, we are getting closer to understand the nature of this disorder in humans – but depressive disorders may not be specific only to humans. Although due to the inability to collect a verbal report from animals and the lack of direct insight into their mental states, the diagnosis of depression in animals is based on behavioural observations, which is considered insufficient to diagnose the disorder. Nevertheless, animal models of depression indicate the possibility of depression-like states in laboratory animals. This review aims to bring together previous reports of depressive disorder symptoms in group-living mammalian species living in unnatural environments and/or experiencing relatively frequent contact with humans: primates, marine mammals, domestic horses and elephants. The paper summarizes previous reports of depressive-like symptoms in those species, pointing out the similarity of depression-like symptoms in aforementioned animals to those observable in human depression. The efficacy of pharmacological treatments indicates that the brain biochemistry of depressive-like states is similar in both laboratory animals and humans. Those symptoms in laboratory animals are similar to certain species of group-living mammalian species – furthermore, the methods for inducing similar states are not uncommon in the training of the aforementioned mammals, indicating similar causes of the phenomenon. All previous reports of Major Depressive Disorder symptoms listed in the DSM-V and noticed in animals were considered and redescribed, such as: loss of interest (anhedonia), sleep disorders, psychomotor retardation, fatigue, feeling worthless, decreased concentration, self-harm and impairment in social. In addition, behavioural changes similar to mourning states resulting from changes in herd structure and stereotypies occurring in captive animals were taken into account. The data collected shows that, based on observed behaviours and similarities to symptoms in laboratory animals, at least some of group-living mammalian species experiencing relatively frequent contact with humans may suffer from depression-like symptoms, which may not only extend the knowledge of depression in humans, but also have a significant impact on improving the welfare of captive animals. Perhaps the only difference found between humans and some animals when it comes to depressive disorder is the ability to verbally report one's internal states.

1. Introduction

According to the DSM-V (Diagnostic and Statistical Manual of Mental Disorders, 5th Ed.; American Psychiatric Association, 2013), Major Depressive Disorder (MDD) is a potentially life-threatening mental illness, diagnosed in up to 8.3 % of the adult population in the United States in 2021 (National Institute of Mental Health, 2023) and 7.2 % in European Union (Eurostat, 2019). Treatment for MDD occurs on multiple levels, and it is not uncommon for pharmacological treatment to be recommended in order to assist in the treatment process or reduce the frequency of troublesome symptoms.

The development of pharmacology inherently involves several stages of testing, often using laboratory animals. In these stages, conditions similar to human symptoms are induced in order to test the efficacy and potential side effects of the substances being examined (Doke and Dhawale, 2013). One way to understand the biological and neurochemical mechanisms of specific disorders, such as MDD, is by creating corresponding animal models (Song and Kim, 2021; Mineka and Zinbarg, 1991).

Despite some claims that a comprehensive animal model of depression, which incorporates all symptoms observed in humans, has not yet been successfully developed (Willner and Mitchell, 2002), it should be acknowledged that these models are still effectively used in expanding our knowledge of the causes, progression, and treatment of depressive

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disorders in animals. To date, three main animal models of depression have been developed: the learned helplessness model, the chronic mild stress model, and the social defeat stress model (Yan et al., 2010).

In recent years, awareness of animal welfare has grown, as evidenced by various societal movements to protect animals and improve their living conditions (e.g., Marino, 2018). This concern extends not only to pets and companion animals but also to zoo animals and those frequently subjected to human training. Animals used in zoological gardens, reserves, or for commercial purposes are of particular concern to the public. Due to safety considerations, ethical concerns, and the difficulty in acquiring a suitable research group, no studies have yet been conducted to deliberately induce depressive disorders in animals such as elephants, marine mammals, or horses. However, studies have been carried out on certain non-human primates, due to significant similarities in their nervous system structure, which may help further understanding and treatment of depression in humans (Qin et al., 2019; Felger et al., 2007; Felger et al., 2013), despite the ethical concerns surrounding these studies (Carvalho et al., 2018).

An increasing number of scientific publications have explored the possibility of clinically diagnosing depression in various animal species (MacLellan et al., 2021; Lecorps et al., 2021; Ausderau et al., 2023; Meijer, 2019). This article aims to further investigate animal behaviour to determine whether a diagnosis of MDD is possible. The main focus will be on reports of depressive-like symptoms that arise not from deliberate induction but as a result of continuous, potentially aversive changes in the animal's living environment. Therefore, this article seeks to review behavioural signs that could indicate clinical depression according to DSM-V criteria in four groups of diverse, yet group-living animals with complex social behaviour and well-documented cognitive abilities: non-human primates, as a species that is somewhat 'intermediate' between humans and other non-human animals; elephants; domestic horses; and certain species of marine mammals, whose behavioural symptoms are not dissimilar to those observed in primates.

2. Methods for literature review

A literature search was conducted in Google Scholar between February and October 2024 to identify peer-reviewed articles concerning spontaneous depressive-like behaviours in selected group-living mammalian species, namely non-human primates, marine mammals, domestic horses, and elephants. Given the relatively underdeveloped nature of this research area, an exhaustive manual search without the use of database filters or advanced operators was adopted to ensure the inclusion of all relevant studies describing behavioural signs of impaired welfare in these species.

Only peer-reviewed articles were considered for inclusion. The exclusion criteria comprised laboratory-based studies, articles concerning unrelated physical or medical conditions (such as dental diseases in cetaceans, gastrointestinal disorders in horses and elephants, or parasitic infections in non-human primates), papers published in non-peer-reviewed or potentially predatory journals, and studies lacking any information about the health or welfare status of the observed animals. Articles dealing with the behavioural signs of decreased welfare of the aforementioned animals were taken into account The selection and eligibility assessments were performed by a single reviewer, and no automation tools were used at any stage of the process.

Articles were grouped thematically, first by animal species, and subsequently by specific behavioural symptoms observed in those species. All possible combinations of phrases corresponding to animal species and symptoms of depressive disorders distinguished in the DSM-V classification and animal models of depression were used to retrieve articles. Phrases used in search took form of "[animal species] [symptom]". The animal species names and symptoms used in the search are presented in Table 1.

As an effect of the search, 151 articles were analysed and 46 were excluded due to inconsistency with the topic, methodological incompatibility, or other reasons stated above (e.g. absence of welfare-related data) or prior inclusion in other meta-analyses. The final corpus comprised studies that fulfilled the inclusion criteria and were thematically relevant. No data extraction software or tools were used. The outcomes of interest were defined as observable depressive-like behaviours identified in the target species. Only well-documented symptoms assessed by trained or qualified observers were included in the synthesis. Due to the novelty of the research area, it was frequently unclear whether certain symptoms were genuinely absent or simply not yet described or misinterpreted in the literature.

Due to the descriptive nature of the studies and heterogeneity of methods, no formal tool for assessing risk of bias was applied. No quantitative effect measures were used, as the review was qualitative in nature. Similarly, no sensitivity analyses were conducted. Data were synthesised narratively, initially grouped by species, and further classified by symptom type. Where relevant, potential differences across species were discussed qualitatively.

Table 1
Terms used in search to identify relevant articles for the review.

Search terms	
Animal Species	Symptoms
Horses	Depression
Dolphins	Depressed mood
Cetaceans	Anhedonia
Marine mammals	Sleep disturbance
Non-human primates	Fatigue
Primates	Psychomotor retardation
Chimpanzees	Psychomotor agitation
Monkeys	Decreased concentration
Elephants	Suicide
	Self-harm
	Self-mutilation
	Chronic mild stress
	Learned helplessness
	Social defeat

2.1. DSM-V criteria of MDD and its animal-interpretation

A significant challenge in diagnosing depressive disorders in non-human animals is the inability to obtain verbal self-reports. This limitation is compounded by the inherent subjectivity of symptoms, which also complicates diagnosing Major Depressive Disorder (MDD) in humans (Gupta, 2009). However, certain symptoms, such as significant weight changes, psychomotor agitation or retardation, and reduced concentration, can be assessed objectively in humans through physical examination and cognitive testing. Depressed mood and anhedonia are evaluated using behavioural questionnaires (Gupta, 2009).

For animals, tools have been developed to identify welfare disorders by assessing behavioural changes relative to healthy or free-living counterparts. Using detailed DSM-V criteria, symptoms have been adapted into behavioural assessments applicable to various animal species (Table 2). In human diagnostics, the presence of MDD is established if at least five of nine symptoms are present for a minimum of two weeks, with at least one being either depressed mood or loss of interest/pleasure (anhedonia). In order to maintain theoretical correspondence between human and animal depression and assuming no major temporal scale differences between species, it would be beneficial to maintain in the animal studies the same criteria regarding symptom duration, severity, and number of occurrences. Social impairment is a particularly observable symptom in herd animals, where depressive-like behaviours disrupt normal group dynamics. This mirrors depression's effects on human social functioning (Kupferberg et al., 2016).

1. **Depressed mood** Depressed mood is a crucial criterion for the diagnosis, but it might be difficult to observe objectively in non-human animals – for example, tears in most animal species are not

Table 2
DSM-V criteria for MDD and their interpretation for use in non-human animals.

	DSM-V criteria	Human symptoms	Potential non-human symptoms
1.	Depressed mood	Indicated by subjective report (feels sad, empty, hopeless) or others' observation (seems tearful, in children and adolescents: also irritable mood)	no obvious symptoms, inability to obtain a verbal report
2.	Anhedonia	Decreased ability to experience pleasure from positive stimuli/ loss of pleasure previously experienced	Lack of interest in sucrose intake
3.	Weight gain or lose	Also decrease or increase in appetite	Weight disorders co-occurring with reduced well-being not directly caused by other health problems
4.	Insomnia or hypersomnia	inability to fall asleep/ extended period of sleep	Stress-related sleep disorders
5.	Psychomotor agitation/ retardation	Observable also by others: restlessness, being slowed down	Noticeable slowing down of reactions, changes in emotional expression
6.	Fatigue/Loss of Energy	Sustained fatigue without physical exertion, smallest tasks seem to require substantial effort	Reduced motivation to locomote/ explore the environment/social interaction
7.	Feeling worthless/ excessive/ inappropriate guilt	Individual often misinterpret neutral or trivial day-to-day events as evidence of personal defects	Negative cognitive biases
8.	Decreased concentration	Disminished ability to think or concentrate, indecisiveness,	Lowered cognitive abilities, indecisiveness, inability to maintain attention for long periods of time
9.	Thoughts of death/suicide	Recurrent suicidal ideation/attempt; often connected with previous self-harming	Self-injurious behaviours (SIBs); self-harming (some stereotypies)

associated with sadness, but purely physiological processes and irritable mood cannot be diagnosed in a methodologically accurate way due to the impossibility of isolating external factors that may cause irritation (e.g. annoying insects or incomprehensible commands, Picó, Gadea, 2021). Due to the aforementioned, the main MDD criteria for animals which can be objectively evaluated remain anhedonia.

2. **Anhedonia** In laboratory settings, animals exposed to prolonged stress display behavioural changes, such as reduced sucrose intake, indicative of anhedonia (Katz, 1982). Similar signs are observed in other animals with diminished psychological well-being (Papp et al., 1991). Two principal subtypes of anhedonia can be distinguished: motivational and consummatory. The former refers to a diminished motivation to pursue rewarding stimuli, whereas the latter describes a reduced capacity to experience pleasure during the actual consumption or receipt of a reward (Treadway and Zald, 2011). Apathy—defined as a lack of goal-directed voluntary behaviour (Marin, 1991)—is clinically distinct from depression; however, shared neurobiological mechanisms between apathy and motivational anhedonia have been suggested (Husain and Roiser, 2018; Petelin et al., 2022; Palaric, 2016). Since apathy appears to be a broader construct with its distinct subtypes, it should not be equated directly with anhedonia (Ang et al., 2017). Reports of apathetic behaviours are therefore included in this study, but they are not conflated with anhedonia due to insufficient evidence supporting the interchangeability of these symptoms.
3. **Weight gain or lose** Weight loss or gain in animals may result from decreased interest in food, but other factors such as stress, poor-quality feed, or health issues also influence weight (Bjerkeset, 2004). This review does not include changes in body weight or appetite arising from other pathological conditions or resulting from pharmacological interventions. Nevertheless, instances of eating disorders co-occurring with signs of reduced psychological well-being are presented in this paper.
4. **Insomnia or hypersomnia** Although sleep disorders in animals are often seen to be associated with disrupted diurnal rhythms, excessive stress, herd and health problems, research indicates that sleep deprivation may not be the best diagnostic sign due to the fact that sleep disorders often occur as an independent disease entity, which can be both a symptom of depressive disorders and their cause (Bao et al., 2017; Li et al., 2022; Meerlo et al., 2015; Vargas and Perlis, 2020; Xing et al., 2021). Nevertheless, they will be included in this article because, although there is no consensus on the relationship between sleep disorders and depressive symptoms, they are inevitably associated with emotional deterioration. Sleep disorders in marine mammals are not extensively analysed here due to limited knowledge of their sleep mechanisms (Lyamin et al., 2008).
5. **Psychomotor agitation/retardation** Psychomotor retardation manifested by low arousal and resulting inactivity seems to be associated with depression symptoms (Benning, Oumeziane, 2017) and it can be a symptom of negative affective states experienced also in animals, as indicated by Fureix and Meagher (2015).
6. **Fatigue/Loss of Energy** Fatigue or loss of energy is reported in group-living animals as a lack of motivation to explore the environment, to social interact with other individuals or decreased locomotor activity compared to mentally healthy animals, often leading to social impairment as observed by Williams et al. (2018).
7. **Feeling worthless/excessive/inappropriate guilt** While verbal reporting is impossible in animals, cognitive affective biases (CABs) provide a behavioural alternative for evaluating negative affective states (Smith et al., 2018). Negative cognitive biases co-occur with human depression (LeMoult and Gotlib, 2019; Beevers et al., 2018) and are central to Beck's cognitive triad of depression (Beck, 1976). Pessimistic judgement biases—such as withholding responses to ambiguous cues—may indicate emotional states and could relate also to anhedonia by reflecting an inhibition of reward-seeking behaviour (Disner et al., 2011; Hales et al., 2014). Studies on attention biases suggest that negative emotions narrow attentional focus to potential threats (Crump et al., 2018).
8. **Decreased concentration** Decreased concentration is noticeable in humans, among others, as problems with maintaining focus and attention (Yang et al., 2015) are also noticeable in animals in the form of reduced results in attention tests (e.g. Rochais et al., 2016). Lack of decisiveness is a common description of the behaviour of animals experiencing learned helplessness (Takamori et al., 2001).
9. **Thoughts of death/suicide** The absence of reliable sources confirming cases of suicide in animals is closely tied to the inability to investigate volition and intent—key aspects of human suicide (Preti, 2011). The only credible way to explore the potential presence of such phenomena in animals is to study behaviours that, in humans, are strongly associated with an increased risk of suicide. These include neurobiological and environmental factors underlying stereotypies and self-injurious behaviour, which appear to overlap with mechanisms implicated in suicidality-related traits in humans, such as dysregulation of stress response and neurotransmitter systems (Dwivedi et al., 2017). Despite similarities in clinical presentation, the mechanisms driving the onset of stereotypies in humans and animals differ considerably. In humans, stereotypies typically emerge during early developmental stages, whereas in animals they are acquired behaviours, arising as a consequence of reduced welfare. Many animals kept in captivity start to show abnormal behaviours such as self-mutilations and stereotypies. The development of

Self-Injurious Behaviours (SIBs) is most often the result of inadequate living conditions and chronic stress - it has been postulated that animals develop these behaviours for emotional regulation (Dellinge-Ness, Handler, 2006). The study of these behaviours in non-human primates appears to hold significant translational value for understanding and treating Non-suicidal Self-Injury (NSSI) in humans, which is recognised as a key factor markedly increasing the risk of suicide (Barraclough, Jones, 1978; Meyer, Novak, 2021). The occurrence of this type of behaviour highly correlates with the occurrence of other stereotypic behaviours (Polanco, 2016). Stereotypies are aberrant, repetitive behaviours occurring in animals as a result of failure to cope with frustration, observed almost exclusively in captive animals (Mason, Rushen, 2008). Stereotypic behaviours are often distinguished into whole-body stereotypies and self-directed forms, the latter of which carry a heightened risk of direct self-injury and are therefore considered a subtype of self-injurious behaviours (SIBs). Moreover, stereotypies and SIBs frequently co-occur, as they share several risk factors, including environmental deprivation and stress (Well et al., 2003; Devine, 2024). Because of those types of behaviour are seldom if ever observed in nature, stereotypy is widely recognised as a symptom of reduced animal welfare and their occurrence is used in evaluating the quality of life of animals in captivity, e.g. in zoos (Jacobs et al., 2022). Stereotypes seem to make little sense and often cause secondary damage to the animal's body - in the case of oral stereotypes, the greatest damage can be seen in the bite, while movement stereotypes often overload the animal's bone and muscle structures and result in injuries (Haspeslagh et al., 2013). Stereotypes can also involve the animal's body parts hitting objects in the environment. Contrary to the general assumption, animals do not learn stereotypies from other animals - the frequent co-occurrence of these disorders in animals in one social group is usually the result of unfulfilled same-species needs (Nicol, 2010). Abnormalities in the nervous system due to biochemical or maturation disorders stand out as direct causes of stereotypies. These behaviours, in both humans and animals, are associated with cognitive rigidity and social and sensory isolation (Ridley, Baker, 1982).

3. Results

This article addresses behavioural disorders in animals, focusing on species such as non-human primates, domestic horses, elephants, and marine mammals. These group-living mammalian species are frequently studied in welfare research due to their presence in zoological gardens or their involvement in human activities, making them particularly suitable subjects for examining the effects of captivity on behaviour and mental well-being. To ensure clarity, the data is organised into subgroups based on animal species. Given the frequent references to animal models of depression in the subsequent text, the most significant models are introduced at the outset, highlighting their relevance in identifying specific depressive symptoms outlined in the DSM-V classification.

3.1. Model of learned helplessness (LH)

The learned helplessness model is characterised by depressive-like symptoms, including deficits in behavioural coping, associative learning, and emotional expression. These occur when an individual ceases to attempt avoidance of aversive situations (Lilley et al., 2017). Such behaviours are induced using unpredictable and uncontrollable aversive stimuli, such as electric shocks or other inescapable stressors. Behavioural abnormalities are assessed through paradigms such as the active escape paradigm (Yan et al., 2010).

Neurovegetative changes are also evident, including endocrine disruptions (Greenberg et al., 1989), diminished sexual behaviour, reduced body weight (Dess et al., 1988), and alterations in rapid eye movement (REM) sleep (Adrien et al., 1991). These animal symptoms closely align with those of Major Depressive Disorder (MDD) in humans and can be alleviated using pharmacological antidepressants (Takamori et al., 2001). The learned helplessness model is particularly useful for investigating escape deficits, indecisiveness, and heightened anxiety, often linked to changes in noradrenaline neurotransmission (Song and Kim, 2021). However, its limitations include an inability to address genetic and environmental variables comprehensively, and the model is primarily applicable to specific types of depression, such as post-traumatic depression (Song and Kim, 2021).

3.2. Model of chronic mild stress (CMS)

To address criticisms regarding the transient nature of depressive-like symptoms in the learned helplessness model (Dwivedi et al., 2004), the chronic mild stress model introduces stressors gradually and over an extended period. This approach simulates a more natural induction of chronic depressive-like states (Katz et al., 1981). Laboratory animals subjected to sustained stress exhibit behavioural changes, such as reduced sucrose intake, indicative of anhedonia (Katz, 1982). Other observable effects include reduced physical activity and changes in sexual, aggressive, and investigative behaviours (Yan et al., 2010).

A key advantage of this model is its realistic, multi-factorial approach to stress induction, offering a robust representation of anhedonia and sleep disturbances observed in human depression (Song and Kim, 2021). Despite its alignment with human depressive symptoms and the animals' responsiveness to drug treatments, the model is less frequently employed due to procedural complexity, challenges in replicability, and ethical concerns (Yan et al., 2010).

3.3. Model of chronic social defeat (CSD)

Given that many human stressors are rooted in social problems, the chronic social defeat model seeks to replicate these issues to induce depressive-like states in animals (Keeney and Hogg, 1999). This model effectively elicits symptoms such as social withdrawal, increased anxiety, and apathy—hallmarks of human depression. It also allows researchers to examine differences between susceptible and resilient individuals, thereby aiding the identification of factors that increase depression risk in humans (Song and Kim, 2021).

However, this model faces significant challenges in laboratory settings. For instance, male rats exposed to intimidation by stronger counterparts often exhibit anxiety rather than a depressive-like state, while female rats and mice are generally reluctant to engage in confrontations (Song and Kim, 2021).

Nevertheless the limited space provided to group-living animals and artificially created social structures often result in social impairments, such as inadequate maternal care or social withdrawal (Waples and Gales, 2002). As space constraints increase, the likelihood of conflict rises (Rose et al., 2017). Conflicts frequently stem from unmet species-specific needs, such as insufficient food or space. In such scenarios, many group-living animals, including cetaceans, opt to disperse to avoid escalating aggression (Bisther, 2002).

3.4. Non-human primates

Due to their similarity to humans, many primate species are used in laboratory research. Consequently, numerous studies have been conducted on these species, including investigations into the induction of depression models (Phillips et al., 2014; Nelson and Winslow, 2009; Liddle, 1993). The induction of learned helplessness is a standard approach in behavioural studies of non-human primates, aiming to discover therapeutic interventions that can reverse learned helplessness in species such as rhesus monkeys. This research is crucial for understanding the mechanisms underlying the disorder and drawing analogies to humans (Rush et al., 1983).

When administered to monkeys, corticotropin-releasing factor

increases anxiety and depressive behaviour, particularly in social contexts, as evidenced by huddling, social withdrawal, and fatigue (Strome et al., 2002). Among female cynomolgus monkeys, depressive behaviour is more frequently observed in individuals with lower positions in herd hierarchies. A co-occurring factor is reduced ovarian steroid levels despite regular menstrual cycles, a characteristic under investigation to understand the high prevalence of depression in women (Willard and Shively, 2012).

Spontaneous depressive behaviour is also noticeable, manifesting as reduced physical activity, a distinctive posture (huddling), elevated cortisol levels, and an increased need for physical contact with others (Qin et al., 2015). In rhesus monkeys, cortisol levels are positively correlated with depressive behaviour (Qin et al., 2016). Research by Qin et al. (2019) suggests that chronic mild stress, induced through social and visual isolation, impacts glucose metabolism in both rodents and macaques. These changes mimic human neurobiological processes, including symptoms of anhedonia, reduced dopamine secretion, and decreased sucrose intake. In addition to typical symptoms of anhedonia, depressed cynomolgus monkeys exhibit weight loss despite increased food intake and a depressed posture (Fan et al., 2013). According to Ferdowsian et al. (2011), 58 % of captive chimpanzees display symptoms resembling depression or PTSD, based on alternative diagnostic criteria derived from DSM-IV standards.

Sleep disorders in depressive-like monkeys primarily manifest as hypersomnia, mirroring patterns seen in human patients with depression (Chen et al., 2011). Ketamine is sometimes administered to treat hypersomnia in monkeys, as it extends wakefulness and shortens nocturnal sleep (Li et al., 2022).

In rhesus macaques, pessimistic judgements often occur after veterinary procedures, while environmental enrichment leads to more optimistic evaluations. These findings indicate that emotional states in these animals can be indirectly studied using cognitive bias procedures (Clegg, 2018). Studies using a revised version of the emotional Stroop task have shown that rhesus macaques tend to slow their responses to mildly threatening stimuli following stress, indicating a cognitive freeze (Bethell et al., 2016). In tufted capuchins, pessimistic judgements in Go/No-Go tasks correlate with stereotypies and elevated faecal corticoid levels (Clegg, 2018).

Keeping primates in individual cages, particularly from a young age, results in self-injurious behaviours (SIBs) in 10–14 % of animals. These behaviours are linked to excessive stress, social isolation, and inadequate rearing conditions (Dellinge-Ness and Handler, 2006; Preti, 2007). Early maternal separation significantly increases the likelihood of self-mutilation and decreases social play (Drago and Thierry, 2000) and has been linked to depressive behaviours in adolescent male rhesus monkeys, accompanied by increased cortisol production and weight loss (Zhang et al., 2016). Affected animals exhibit stereotypic behaviours such as pacing, twirling, regurgitation and reingestion, playing with food, or rocking (Ridley and Baker, 1982; Marriner and Drickamer, 1994).

Sensory deprivation and monotony during adolescence often result in abnormal behaviours such as rocking, finger-sucking, and self-mutilation. Captive monkeys sometimes beat themselves so severely that they scream (Morris, 1964; Cross and Harlow, 1965). Chimpanzees exposed to chronic stress may engage in hair-plucking, leading to baldness, which correlates with increased faecal glucocorticoid levels (Lopresti-Goodman et al., 2012; Pizzutto et al., 2015). Macaques may bite, scratch, or strike their bodies against hard surfaces, causing injuries of varying severity.

3.5. Domestic horses

The domestic horse is a species that functions in stable social groups (Hall et al., 2018) and is primarily used in the equestrian business, being stationed more often in studs than in zoos. Due to their highly specialised herding behaviour, the intensive training processes they undergo (McGreevy and McLean, 2009), and observations of learned helplessness (Fureix et al., 2012, 2015), horses remain a valuable research model for studying psychological disorders.

Symptoms of learned helplessness in horses include a withdrawn posture, characterised by a downward-stretched neck, immobile and wide-open eyes, and lowered, backward-facing ears (Hall et al., 2008). Behavioural signs such as prolonged inactivity, reduced response to environmental stimuli, weaker responses to touch, abandonment of environmental exploration (Fureix et al., 2015), fatigue, and a withdrawn posture (Fureix et al., 2012, 2015; Hall and Kay, 2024) suggest depressive symptoms similar to those observed in humans. Severe deficits in cognitive control have also been noted in withdrawn horses. They exhibit reduced responses to auditory stimuli and shorter attention spans, indicating impairments in selective attention functioning (Rochais et al., 2016).

Further evidence of potential depressive states in horses comes from research on food preferences. Studies indicate that horses generally prefer sweetened to unsweetened food (Hawkes et al., 1985). A reduced willingness to consume sucrose, along with other behavioural symptoms, suggests the possibility of depressive symptoms, with observed food preferences in withdrawn horses potentially indicating anhedonia (Fureix et al., 2015). Additionally, apathetic behaviour in horses is considered a key indicator of their welfare (Lesimple, 2020).

Sleep patterns also play a crucial role in equine welfare and mental health. Domestic horses can rest while standing. However, REM sleep is possible only when they lie down, highlighting the importance of providing a suitable environment that allows comfortable rest in this position (Carson and Wood-Gush, 1983). Isolation and insecurity caused by the absence of a herd, excessive stress, or environmental changes are common causes of sleep deprivation in horses. These factors often coexist with health problems, such as joint damage, particularly in older individuals (Greening and McBride, 2022). The conditions in which horses are kept also directly affect the frequency with which they lie down to sleep and, consequently, the amount of REM sleep they experience (Greening et al., 2021).

Disruptions in sleep patterns are closely linked to the development of stereotypies and other abnormal behaviours - some stereotypies in horses are associated with altered nocturnal activity patterns (Clegg et al., 2008). Narcolepsy, a state of excessive drowsiness secondary to recumbent sleep deprivation, leads to partial motor collapse (Bertone, 2006). Narcoleptic attacks often cause significant injuries resulting from uncontrolled falls (Fuchs et al., 2016). McDonnell (2008) categorised self-mutilation in horses into three types. The first type includes self-injurious behaviours in response to intense or chronic psychological distress, such as gastric ulcers, bladder disease, or abdominal pain. Examples include biting the sides of the body, kicking, and striking the abdomen. The second type, often observed in young stallions, involves aggressive or self-injurious behaviours (Dodman et al., 1994). Limited social contact, an unenriched environment, and insufficient feed are common causes of the third type of stereotypies, which are closely associated with repetitive behaviours such as weaving (Mills, 2005), cribbing (Wickens and Heleski, 2010), wind-sucking, box-walking (McGreevy, 1995), and self-biting (McDonnell, 2008). These behaviours often result in bodily harm, and certain stereotypies, such as cribbing, resemble obsessive-compulsive disorders in humans, being linked to reduced β-endorphin levels (Gillham et al., 1994).

Beyond these behavioural manifestations, cognitive biases provide additional insight into the emotional states of those animals. Horses may also exhibit negative cognitive biases, manifested through "pessimistic" interpretations of ambiguous stimuli. In a cognitive task involving exploration of a bucket placed in an ambiguous location, horses with negative biases took longer to approach the bucket, even when it contained neutral or positive food stimuli (Henry et al., 2017).

3.6. Elephants

Elephants are the least-studied animal group detailed in this article due to methodological challenges, geographical barriers, and the limited number of individuals available for behavioural studies (Gross and Heinsohn, 2023; Turkalo et al., 2018; Webb et al., 2020). Most elephant studies have focused on rescued individuals and those in zoos. Nonetheless, research on these animals highlights their exceptional perceptual and cognitive abilities (Byrne et al., 2009; Hart et al., 2008; Plotnik et al., 2010) as well as their highly advanced social behaviours (Vidya and Sukumar, 2005; Barrett and Benson-Amram, 2021).

Chronic stress, such as that caused by frequent human visitors in zoos, significantly impacts elephant behaviour. Increased human presence elevates stress levels, leading to reduced locomotor activity. Additional stressors, including overstimulation from multiple stimuli, often result in herd conflicts and increased stereotypic behaviours (Fugl et al., 2022). Zoo keepers report that stressed elephants frequently display fatigue, characterised by reduced exploratory and locomotor activities and frequent apathy (Mason and Veasey, 2010; Williams et al., 2018). Welfare assessment tools for elephants classify behaviours such as lethargy, disinterest in the physical environment or social companions, and a hunched or slumped posture as abnormal and indicative of depressive-like moods (Mason and Veasey, 2010; Yon et al., 2019). While no obvious signs of anhedonia have been observed beyond apathy, studies have yet to investigate sucrose preference in elephants with reduced welfare.

In captivity, elephants often display stereotypic behaviours, including body swaying, trunk swaying (Rees, 2009), pacing (Greco et al., 2017), and head bobbing. These behaviours are linked to spatial constraints, monotony in unenriched environments, stress from training, and isolation (Greco et al., 2016). Stereotypic behaviours, such as body swaying, have been associated with a reduction in blood cortisol levels (Kelling, 2008; Meehan et al., 2016; Wells and Irwin, 2008; Mason and Veasey, 2010). Notably, once released into their natural habitats, captive elephants no longer exhibit these stereotypic behaviours (Pretorius et al., 2023).

Social and environmental stressors, such as unrelated individuals in herds, companion loss, inadequate sleeping conditions, and changes in management schedules (e.g., altered meal or training times), contribute to significant sleep deprivation in elephants (Evison et al., 2020; Koyama et al., 2012). Elephants may avoid lying down due to insecurity in new environments, social conflicts, or joint pain, which is sometimes linked to prior stereotypic behaviours. Prolonged lack of recumbent sleep can lead to episodic falls, similar to those observed in domestic horses, potentially causing physical injuries (Schiffmann et al., 2018).

In addition to these physiological and behavioural consequences, inappropriate social development, such as the absence of all-male socialisation, negatively impacts the neurobiological development of elephants, resulting in future aggression problems (Bradshaw and Schore, 2007). Such issues include infanticide and hyperaggressive behaviours toward other elephants (Poole and Granli, 2008). Insufficient social development in female elephants affects maternal skills, leading to frequent infant neglect. Younger elephants are particularly prone to developing stereotypic behaviours when deprived of socialisation, further highlighting the critical role of housing conditions in their neuropsychological development (Varadharajan et al., 2016; Gruber et al., 2000). Beyond these behavioural and cognitive aspects, some studies suggest that elephants may possess a concept of death, as evidenced by the increased time they spend investigating the bodies of deceased conspecifics compared to remains of other species (Douglas-Hamilton et al., 2006).

3.7. Marine Mammals

Chronic and/or intense stress in captive marine mammals manifests through symptoms resembling learned helplessness. These include a lack of behavioural responses to stimuli and environmental changes, reduced interest in new objects, and decreased engagement in social interactions (Delfour and Charles, 2021; Lilley et al., 2017). Additional symptoms include diminished motivation to learn or explore, difficulty maintaining weight, and immune system dysfunction (Waples and Gales, 2002). Animals experiencing so-called depressive-like states often display impaired locomotor activity, with prolonged periods of immobility at the water's surface or excessive resting at the tank's bottom (Ugaz Ruiz et al., 2013). In bottlenose dolphins, passive swimming, such as floating, is sometimes identified as a form of apathy. However, studies have found no strong correlation between floating and reduced motivation (Ames et al., 2024; Clegg et al., 2018). Chronic stress also leads to reduced appetite and weight loss, which can result in secondary health issues that affect lifespan in captivity (Lott and Williamson, 2017).

In studies of marine mammals, cortisol levels are more commonly measured in blubber than in blood due to the invasiveness of blood collection. Blubber samples provide satisfactory results (Newman et al., 1994; Galligan et al., 2018), and tissue cortisol concentrations appear to be linked to stress levels rather than diet (Kucheravy et al., 2022; Busqueta et al., 2020; Trana et al., 2015; Desportes et al., 2007).

Stereotypical behaviours commonly observed in captive marine mammals, such as bottlenose dolphins, include oral actions like biting, chewing, and jaw-popping on steel surfaces. These behaviours can lead to severe dental issues, including infections and secondary occlusal dysfunctions that impair food intake (Jett et al., 2017). Additionally, behaviours such as head-banging against objects have resulted in fatalities due to brain damage (Marino, 2020).

In spatial localisation tests, bottlenose dolphins with reduced psychological well-being displayed slower reaction times to ambiguous stimuli. In contrast, other individuals responded faster and were more likely to swim synchronously (Clegg et al., 2017). Cetaceans with an optimistic outlook were also more likely to engage in synchronous swimming, an affiliative social behaviour crucial for their welfare (Clegg et al., 2017). Research by Clegg and Delfour (2018) showed that bottlenose dolphins exhibiting anticipatory behaviour during training sessions tended to make more pessimistic judgements about near-positive ambiguous cues, indicating emerging negative emotional states.

Due to their unique unihemispheric sleep adaptation, marine mammals can maintain continuous vigilance while resting. This adaptation, essential for breathing at the surface and conserving heat in water, results in minimal REM sleep (Lyamin et al., 2008). While one hemisphere exhibits slow-wave activity, the other remains in a waking-like state. Little is known about the effects of sleep deprivation in these species (Lyamin and Siegel, 2019).

Captive marine mammals, compared to their wild counterparts, exhibit higher levels of aggression toward humans. In the wild, such attacks typically occur only when humans initiate contact with sensitive body areas (Scheer, 2010). However, in captivity, particularly among dolphins trained to interact with humans, aggression is more frequent. Such incidents often involve biting or striking, with some injuries requiring hospitalisation (Rose et al., 2009).

Social withdrawal in captive animals often manifests as anti-social behaviours, including aggression toward others (Lott and Williamson, 2017). Captive orcas, for instance, display aggression not only toward humans but also toward conspecifics (Marino et al., 2020). Orcas in captivity frequently neglect their offspring, which contrasts with the strong mother-offspring bonds seen in the wild, where family groups help rear the young (Marino et al., 2020).

Some marine mammals, particularly dolphins, exhibit caregiving behaviours toward deceased individuals, such as carrying their bodies, attempting resuscitation, or keeping the body afloat. However, it remains unclear whether these actions stem from mourning or an inability to accept death (Bearzi et al., 2018).

4. Implications

In each of the species listed, several DSM-V-compliant signs of depressive disorders can be identified. Non-human primates and domestic horses display seven out of eight symptoms, marine mammals display five out of eight symptoms, and elephants fulfil almost four out of eight criteria (Table 3). The lower number of criteria met in elephants and dolphins can be attributed to several factors. These include a lack of relevant studies on sucrose intake in these species (despite observed apathetic behaviour in elephants that may be connected with anhedonia), limited research on how cognitive task performance relates to elephants' behavioural profiles, and insufficient knowledge about sleep patterns in marine mammals. The lack of published research does not allow the assumption that the given abnormalities occur in these animals - as science develops, more and more data should become available.

The findings suggest that non-human primates and domestic horses may meet the DSM-V criteria for a clinical diagnosis of Major Depressive Disorder (MDD). Marine mammals are also very likely to have this disorder due to meeting the criterion of the presence of a minimum of five symptoms, although the lack of research on the key criterion of anhedonia does not allow a clear statement on the possibility of a correct diagnosis. The lack of sufficient research on elephants prevents a full diagnosis of depression, although the symptoms indicated are a strong indication of the possibility of its occurrence - the possibility of anhedonia needs to be investigated in both species.

Despite the lack of intentional induction of depressive states in large group-living animals due to ethical concerns among others, observed behaviours are consistent with symptoms occurring with induction of depressive models in rodents and some primates indicating that spontaneous depression may develop. Typical depressive symptoms consistent with the animal model of learned helplessness have been observed in non-human primates, domestic horses and partially in marine mammals. For elephants and marine mammals, reports highlight behavioural changes linked to chronic stress. While these studies did not directly compare their findings to the animal model of depression, the documented symptoms align with the chronic mild stress model. A fully developed social defeat model does not seem to have been observed among captive non-laboratory animals - as a result of the onset of aggressive behaviour towards other animals, aggressive individuals are often isolated out of concern for others health (Davis et al., 2009; Williams et al., 2019; Harvey et al., 2018; Scott et al., 2005; Fureix et al., 2012; Hartmann et al., 2009), from where the lack of results regarding the direct effects of aggression on more submissive individuals may stem, although there are noticeable behaviours related to social exclusion and unwillingness to interact with other animals caused by excessive environmental stress. In non-human primates, domestic horses and elephants with co-occurring depressive symptoms, it is observable to adopt a withdrawn posture, noticeable by other individuals.

The occurrence of abnormal behaviour in all the mentioned group-living animal species was influenced by the same factors. These include limited and unenriched living environments in captivity, disruption of animals' natural diurnal rhythms, and training demands, including those related to veterinary or experimental activities. A particularly significant factor is social isolation, whether in adulthood or as a result of impaired juvenile development due to early maternal separation or inadequate socialisation (Lecorps et al., 2021). Overexposure to stress contributes to dysfunction in the HPA axis and consequently increase blood or blubber cortisol levels (Darcet et al., 2016) what was observed in all studied animals in this paper and resembles elevated cortisol levels which can be used to distinguish between depressed and non-depressed human patients (Burke et al., 2005; Sahu et al., 2022). However, due to its low specificity, cortisol level nor other biological parameters should not be regarded as an independent indicator of depression without the concurrent consideration of other behavioural symptoms (Pariante, Lightman, 2008). Along with the presence of stereotypy or other depressive symptoms, an increased frequency of social impairment among animals was also noticeable, most commonly manifested by increased aggressiveness, which in humans might be one of the consequences of suffering MDD (Venkatesan and Gopalakrishnan, 2023; Liu and Cole, 2021; Knox et al., 2000). Such strong and similar behavioural responses across these diverse species correspond with their advanced cognitive abilities. This high level of cognitive development likely facilitates the emergence of complex emotions and the formation of affective states (Clegg et al., 2017).

Self-consciousness seems to be an important factor in the development of clinical depression in humans (Hull et al., 1990; Smith and Greenberg, 1981; Whiteley, 2021). Additionally, diagnosing depression requires verbal reports to assess subjective emotional states, and there are inherent challenges in translating specific symptoms across species due to biological differences (Harro, 2018). Therefore, it is unsurprising that attributing the same disorder to non-human animals encounters resistance. Beyond diagnostic challenges, the debate often centres on the question of animal self-consciousness (Bekoff, 2003; Birch et al., 2020). However, Bekoff and Sherman (2004) argue that self-consciousness is more likely to develop in highly social species, where both intra- and interspecific cooperation are crucial. Examples of species that form advanced social structures are in fact aforementioned non-human primates, domestic horses, elephants and marine mammals.

Some researchers propose that depression serves as an adaptive strategy, promoting risk avoidance through reduced reward system activity, social withdrawal, and signalling a need for support (Badcock et al., 2017; Schäfer et al., 2016). An adaptive function of depression may be thought to conserve energy which results in a decrease in activity due to aversive experienced events (Beck and Bredemeier, 2016), as Darwinian models of depression suggest, that the condition may have developed as a result of uncontrollable, aversive events (Allen and Badcock, 2006). However, depressive behaviour should then be effective in supporting social problem solving, and in fact it leads to a reduction in cognitive and social abilities (Nettle, 2004). Dysregulation

Table 3
Presence of merged depressive symptoms from DSM-V and own interpretation in non-human primates, domestic horses, elephants and marine mammals.

Depressive symptoms	Group of species			
	Non-human primates	Domestic horses	Elephants	Marine mammals
Anhedonia	Yes	Yes	Apathy	No data*
Weight lose	Yes	No**	No**	Yes
Insomnia or hypersomnia	Yes, Hypersomnia	Yes, Insomnia ***	Yes, Insomnia ***	No data
Psychomotor retardation	Yes	Yes	No data	Yes
Fatigue/Loss of Energy	Yes	Yes	Yes	Yes
Feeling worthless (Negative cognitive biases)	Yes	Yes	No data	Yes
Decreased concentration	No data****	Yes	No data	No data
Thoughts of death/ suicide (self-harming, stereotypes)	Yes	Yes	Yes	Yes

* despite reports of possible apathetic behaviour, there is too little data to fully confirm

** weight changes in is often associated with gastrointestinal diseases or inadequate feed supply and quality (e.g. in horses: Andrews et al., 2005), there are no data on the direct or indirect effect of depression on body weight changes

*** insomnia as a result of excessive stress and failure to provide adequate living conditions

**** no data showing reduced concentration in spontaneously occurring depressive disorders in these species

models of depression are more widely accepted, suggesting that depression is not inherently adaptive but arises from the malfunction of mechanisms originally designed to be beneficial, such as reduced activity in response to failure or rumination (Nesse, 2000; Sloman et al., 2003; Gilbert and Allan, 1998). This perspective aligns with observations in animals, particularly socially skilled species, where disruptions in emotional reactivity can lead to depressive symptoms (Neumann, 2009).

A key diagnostic criterion for depressive disorders is the persistence of abnormal behaviours – however, most studies fail to specify the duration of these behaviours, particularly in reports on captive animals. Although the described cases of depressive symptoms involved captive animals with constant living conditions, more longitudinal studies on such animals are still needed to confirm the constancy of symptoms over time.

Nevertheless, this article argues for the feasibility of diagnosing Major Depressive Disorder in large group-living animals using DSM-V criteria. By examining the causes, symptoms and the consequences in terms of social impairment this study not only aims to improve animal welfare but also to advance research on animal models, thereby enhancing our understanding of this disorder in humans. What is very important, this review takes into account the possibility of the occurrence of depressive symptoms in animal species, but did not confirm the occurrence of all mentioned symptoms in a single individual of a given species - there is certainly a need for not only more reports on long-term behavioural evaluations of captive animals, but especially more detailed case descriptions of animals with suspected depressive disorders. A compelling argument for the emergence of spontaneous depression in non-human primates, domestic horses, elephants and marine mammals will be to increase the accuracy of the research by evaluating other depressive symptoms, analysing the animals' behaviour with regard to their health conditions and welfare conditions.

5. Conclusion

This study highlights the feasibility of applying DSM-V criteria to assess depressive symptoms in group-living mammalian species, including non-human primates, domestic horses, elephants and marine mammals. By identifying several symptoms consistent with Major Depressive Disorder (MDD) across these species, the findings emphasize the need for more comprehensive and longitudinal research on animal behaviour and mental health. Key factors contributing to the emergence of depressive symptoms, such as social isolation, limited environmental enrichment and chronic stress underline the critical role of improved welfare conditions in mitigating these issues.

The implications of this study extend beyond animal welfare, offering valuable insights into the mechanisms of depression in humans by refining animal models of the disorder. Enhanced understanding of spontaneous depressive symptoms in animals may contribute to therapeutic approaches, better diagnostic tools and overall welfare for captive animals. The findings also call for detailed case studies and a deeper investigation into long-term behavioural patterns to substantiate the spontaneous occurrence of depression in several mammalian species. By bridging gaps in knowledge, this research aims to improve the well-being of animals while fostering advancements in understanding depression as a shared condition across species.

CRediT authorship contribution statement

Ida Ilmer: Writing – original draft, Investigation, Conceptualization. **Tomasz Smoleń:** Writing – review & editing, Supervision, Conceptualization.

Declaration of Competing Interest

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

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