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Animal Welfare 2022, 31: 99-111
ISSN 0962-7286
doi: 10.7120/09627286.31.1.009

Linking the roles of personality and stress physiology for managing the welfare of captive big cats

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Abstract

Animal welfare is important for the humane treatment of animals under our care. Zoos and rescue centres manage various charismatic animals, such as big cats, with limited resources. It is therefore essential for caretakers to understand the needs of an individual big cat to ensure its welfare. However, these needs may differ due to a big cat's personality, which may be identified by its coping style in a stressful situation. In addition, stress is one of the major factors affecting animal welfare. There is limited evidence showing strong associations between personality and stress physiology in big cats. This review focuses on the integration of personality and stress physiology of captive big cats, to highlight possible improvements in their husbandry. Our review identifies key factors that may influence big cat responses to stressors. These influencing factors include: i) social interactions; ii) environment; iii) life history and evolutionary traits; iv) genetics; and v) health. The first two factors are relatively well covered in the literature; however, the final three are potentially very promising avenues for future research to better understand how we can improve big cat welfare.

Keywords: *animal personality, animal welfare, coping style, glucocorticoids, individual variation, stressors*

Introduction

Animal welfare is important for the humane treatment of animals under our care. Concerns around animal welfare began in the mid-1960s for the physical and mental well-being of farm animals (Harrison 1964; Brambell 1965). Zoos and rescue centres manage various charismatic animals, including big cats, with limited resources and the Five Domains Model of animal welfare provides guiding principles for overall animal welfare (Mellor 2017). However, the 'one size fits all' welfare strategy, where animals are viewed at a species level, may not promote the best welfare outcome for every individual (Wolfensohn *et al* 2018). Thus, the welfare indicators may vary between individual big cats, and animal personality is recognised as a key factor contributing to this variation (Mason & Mendl 1993; Finkemeier *et al* 2018).

Personality is defined as the set of behaviours exhibited consistently across time and situations (Koolhaas *et al* 1999; Réale & Dingemanse 2012; Finkemeier *et al* 2018). Psychologists studying human behaviours use this knowledge to better understand how people react and respond to different situations (Gosling & Mehta 2013). It is further interpreted as an approach to help individuals make better life choices. Similarly, exploring big cat personalities can help to tailor and make better management decisions to improve the quality of an animal's life. It is accepted that big cats have personalities, with Wielebnowski (1999) likely being the first to describe the personality traits for captive cheetahs (*Acinonyx jubatus*). As situations and times change, an individual's behaviour may change. For example, a behavioural reaction test with a mirror image stimulation showed that anxious clouded leopards (*Neofelis nebulosa*) hid more in a nest-box compared to calm individuals (DeCaluwe *et al* 2013). Thus, the personality of an animal can influence how they cope with negative events in their lives and understanding these individual responses can help improve their welfare. These psychological factors can work synergistically to provide insights into how an animal perceives its environment, including potential stressors (Torgerson-White & Bennett 2014; Finkemeier *et al* 2018).

Wildlife face a range of stressors in captivity, such as capture, human presence, novel environment, climatic changes, or artificial conditions (Clubb & Mason 2003;

Morgan & Tromborg 2007). A stressor can be any challenge or change that occurs in the life of an animal that initiates a neuroendocrine stress response involving the release of stress hormones called catecholamines (rapid flight-fight response) and glucocorticoids (slow responding stress endocrine response) with acute or chronic effects (Selye 1973; Schneiderman *et al* 2005). However, the way an animal perceives these stressors may vary due to their personality and certain personality traits may help big cats cope better. For example, an animal's tendency to hide often demonstrates fearfulness and has previously been correlated with higher stress levels in clouded leopards (Wielebnowski *et al* 2002). Thus, there is a variation in responses and this variation can indicate a big cat's tolerance level depending on its behavioural and physiological coping strategies (Koolhaas *et al* 1999).

Though strong associations have been found between personality and their reaction to stressors in humans and non-human primates, limited integrated research has been conducted for big cats. Despite knowing the benefits of making changes according to the animal's needs, an understanding of what factors play a role in influencing the relationship between its personality and stress physiology is still lacking. Identifying and understanding how the personality of big cats may predict stress responses, is likely to promote more positive welfare outcomes for captive and rescued big cats. This review focuses on three essential topics to understand the underlying mechanisms of personality and stress physiology of big cats by: i) exploring the past literature on big cat personality and stress physiology for the overall scope; ii) establishing the links between integrating these studies; and iii) identifying the factors influencing the relationship of personality and stress physiology in big cats. To conclude, we highlight the limitations of big cat personality and stress physiology research with future avenues for improvement. Understanding how these mechanisms act jointly may identify personalities best suited to cope with the suite of stressors involved in captivity and increase our knowledge to benefit captive or rescued management.

Recent and historical advances in big cat personality research

Most early personality research focused on understanding the different human personality traits and their application to daily life (Gosling & Mehta 2013; Gartner 2017). Later, studies of animal personality started becoming documented in numerous disciplines, but most of it was focused on non-human primate personality (Freeman & Gosling 2010). It took a while for researchers to become comfortable with ascribing personality traits to other animal species, even though the anatomy and physiology of humans were considered similar to that of animals (Gosling & John 1999). This led to the realisation that there were many benefits of understanding the personality of companion and farm animals that could be beneficial to humans (Finkemeier *et al* 2018). Further, this was extended to exploring the personality of other wild animals (Clary *et al* 2014).

Humans have been intrigued by felid behaviours which led to studying domestic cats' personality in the 1980s (Feaver *et al* 1986; Gartner 2017). Many past studies on domestic cats and primates have informed researchers' current knowledge of felid personality traits and have been used to explore big cat personality (Wielebnowski 1999; Phillips & Peck 2007; Baker & Pullen 2013; Chadwick 2014; Torgerson-White & Bennett 2014). Early studies on animal personality suggest that animals have either proactive or reactive coping styles, defined as behavioural and physiological efforts to overcome any aversive situation (Koolhaas *et al* 1999). Proactive individuals tend to show more dominant and bold behaviours, being more aggressive towards conspecifics, while reactive individuals show submissive behaviours and are less explorative (Carere *et al* 2005). Over the years, these early contributions have advanced to incorporate many behaviours forming a robust and reliable felid personality checklist (Gartner *et al* 2014).

Recent and historical advances in big cat stress physiology research

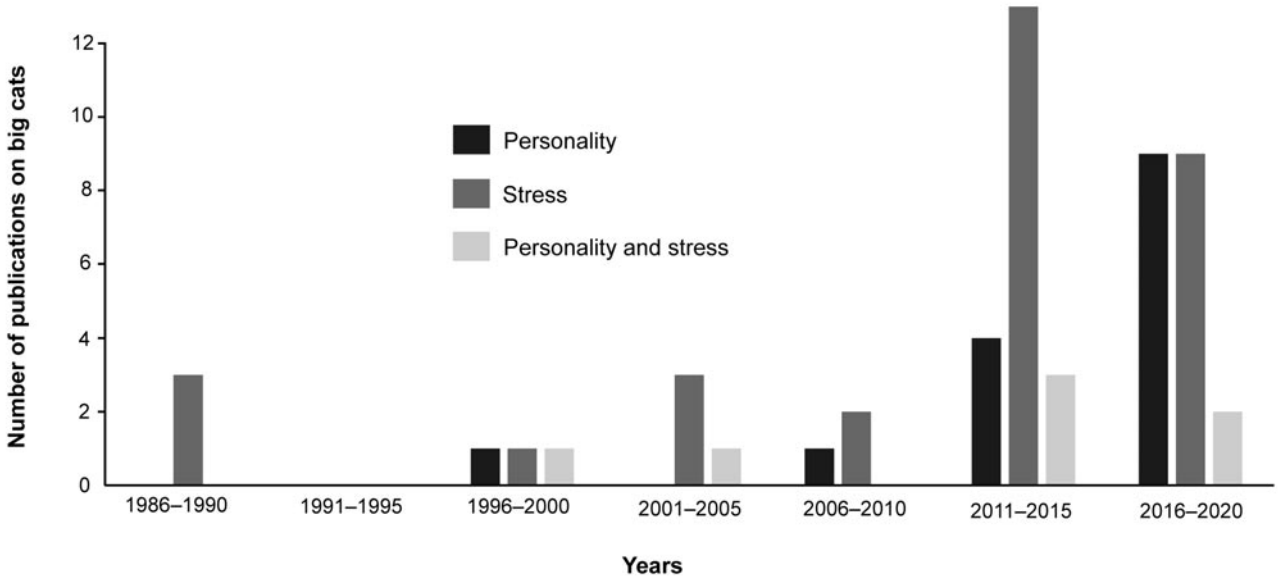
Stress is one of the major factors affecting the welfare of captive animals and the impact of any stressor depends on the way it is perceived by an animal (Morgan & Tromborg 2007; Cockrem 2013). A stressor can disrupt the physiological balance, but stress responses form part of the process of allostasis, which collectively enables the body to achieve a steady internal state (Korte *et al* 2007). Thus, the magnitude of stress is often measured by the degree of an animal's adaptation and coping style (Koolhaas *et al* 1999).

Stress physiology has been extensively studied for big cats with the first published use of the word 'stress' in 1987 to describe cortisol levels among cheetahs (Wildt *et al* 1987) (Table 1; see supplementary material to papers published in *Animal Welfare*: https://www.ufaw.org.uk/the-ufaw-journal/supplementary-material). Exploring stress levels through glucocorticoids first began with invasive procedures where animals were culled to weigh their adrenals (Cannon 1914). Later, this was carried out via surgically implanted infusion pumps for blood and plasma samples (Brown *et al* 1988; Nogueira & Silva 1997). Less invasive procedures using saliva, urine and faecal samples have now been developed (Palme *et al* 2005; Sheriff *et al* 2011). Thus, the recent advances in stress physiology are trending towards developing non-invasive techniques, where stress is studied by minimally coming in direct contact with the animal or without exposing them to any additional stressors.

Previously, the data on individual variation in physiological responses were considered as statistical 'outliers' because some fell outside the normal mean range, yet they could indicate specific information for individual animals (Williams 2008). This is now changing, as studies are including individual animals' stress response to improve individual welfare, thus advancing overall welfare.

https://doi.org/10.7120/09627286.31.1.009 Published online by Cambridge University Press

Figure 1



Changing trends on published big cat personality and stress physiology research.

Contributions of big cat research to the field of animal personality and stress physiology

The literature was mined using key terms in Google scholar, Web of Science, Springer and Scopus databases. For this review, we have included big cats belonging to the subfamily *Pantherinae* (such as tiger [*Panthera tigris*], lion [*Panthera leo*], leopard [*Panthera pardus*], jaguar [*Panthera onca*], snow leopard [*Panthera uncia*], clouded leopard) and large-sized cats of the subfamily *Felinae* (such as cheetah, puma/cougar [*Puma concolor*] and lynx [*Lynx canadensis*]). The combinations of keywords used were 'big cat welfare', 'animal personality' AND 'big cat personality', 'large felid personality', 'wild cat personality', 'temperament, boldness, shyness, individual difference, individual variation' AND 'tiger, lion, leopard, jaguar, snow leopard, clouded leopard, cheetah, lynx, puma/cougar', 'big cat stress physiology', 'HPA-axis, glucocorticoids, cortisol, corticosterone' AND big cats, 'coping style' and 'wild cat stress', along with the scientific names of species.

Peer-reviewed and unpublished thesis articles specifically focusing on big cat personality and stress physiology were identified and reviewed. Though we have excluded smaller wild cats and domestic cats from our literature search, we have cited some particularly relevant to the review. Between 1987 and 2020, 53 papers were identified that studied the personality and/or stress of big cats. These data were arranged chronologically by publication date to show changing trends over the years (Figure 1). Out of the 53 research articles, 15 focused on personality, 31 on stress physiology, and seven studies explored the relationship between personality and reaction to stressors (Jurke *et al* 1997; Wielebnowski *et al* 2002; DeCaluwe *et al* 2013; Torgerson-White & Bennett 2014; Bertocchi *et al* 2015). These papers were thoroughly examined to collect information on the sample size, species, origin of the big cat and the methodology adopted to conduct the study. Lastly, we highlighted five key underlying factors that were commonly discussed across the literature (Table 1; https://www.ufaw.org.uk/the-ufaw-journal/supplementary-material).

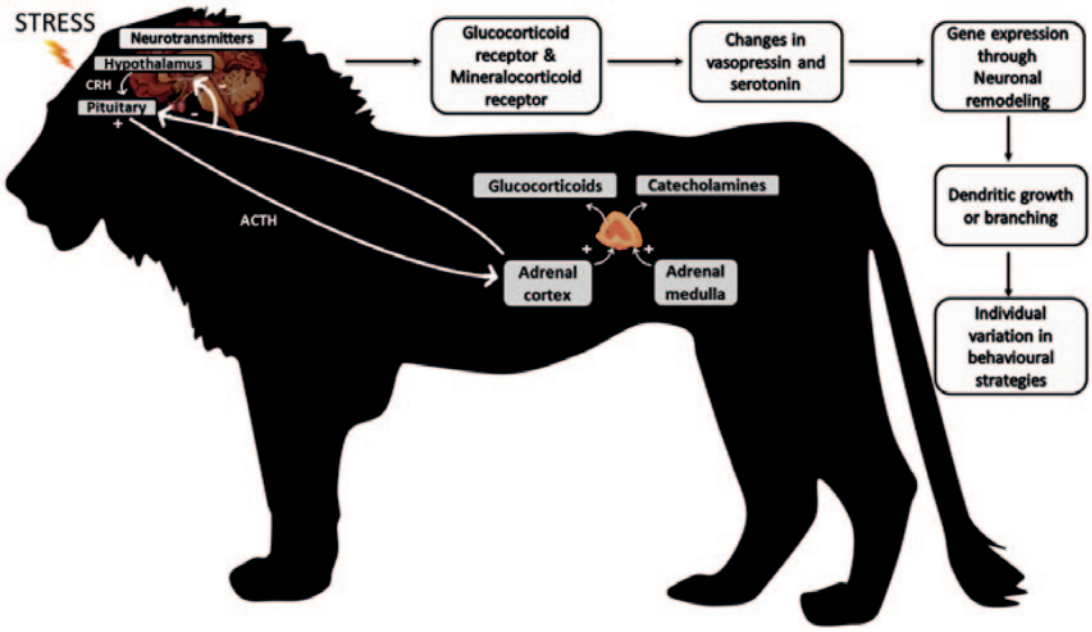
Assessment and application of personality and stress physiology studies in the management of big cat welfare

Personality

Over the years, studies on the personality of domestic cats (*Felis catus silvestris*) have resulted in developing a comprehensive checklist of wild felid personality traits (Gartner *et al* 2014; Phillips *et al* 2017). Most articles have typically used either behavioural ethogram observations, keeper surveys or the introduction of novel objects as methodologies for personality data collection. While considering the previous limitations such as reliability of observer rating, Intra-class Correlation Coefficients (ICC) were used to measure the reliability of raters to avoid any disagreement among them (Shrout & Fleiss 1979). Further, the data were analysed using Principal Component Analysis to determine the personality dimension the animals fall into (Johnson & Wichern 2007).

As many animals fall in the middle of being extremely bold or shy, big cats were classified on scales such as nervous-calm, neurotic-impulsive depending on their coping style (Koolhaas & Van Reenen 2016). There is also variation among the different species of big cats; for example, captive cheetahs are typically assessed as being nervous, adven-

Figure 2



The stress physiological pathway when a big cat is exposed to stressors; adapted from Matteri *et al* (2000) and Caramaschi *et al* (2013).

turous, and aggressive, whereas tigers were noted for being aggressive, fearful, vigilant and/or obedient (Phillips *et al* 2017). The most comprehensive method to assess felid personality was developed by Gartner *et al* (2014) and trialled for various wild cats, such as Scottish wildcat (*Felis silvestris grampia*), clouded leopard, snow leopard and African lion. However, research suggests that studying the personality of big cats has some limitations if studied by itself (Torgerson-White & Bennett 2014), and hence there is a need to critically understand how personality helps an animal to overcome stressors. Some personality traits, such as boldness or shyness, are known to be linked to how animals experience stress (Caramaschi *et al* 2013; Finkemeier *et al* 2018). The personality of an individual may thus affect its coping capacity in a novel environment, which indirectly affects their stress physiology (Koolhaas *et al* 1999).

Stress physiology

The methods for assessing stress physiology have adapted over the years to develop minimally invasive techniques for testing glucocorticoid hormones in biological samples, such as saliva, urine and faeces with a radioimmunoassay (RIA) or enzyme immunoassay (EIA). A stressor leads to a non-specific physiological stress response causing the activation of two 'stress axes'; the hypothalamo-pituitary-adrenal (HPA) and the sympathetic-adrenomedullary (SAM) of the nervous system in vertebrates (Cannon 1914; Selye 1973). This activation leads to the secretion of stress hormones called glucocorticoids which are released in the form of cortisol and corticosterone (Sapolsky *et al* 2000; Oakley & Cidlowski 2013). These glucocorticoids get transported by the blood, and its metabolites can be found elsewhere in the body. The glucocorticoids follow a pathway that can lead to changes in the gene expression when exposed to stressors constantly (Figure 2).

Stress levels can vary in an individual and fluctuate depending on time of day, health status, age, sex, personality, body condition, time of year, stage of breeding and the environment, all of which can influence the coping capacity of an animal (Moberg 1985). Considering this, collecting baseline data, and comparing it to an animal's changing glucocorticoid level will give a better understanding if animals are undergoing acute or chronic stress. Further, this could lead to addressing the underlying issues faced by big cats and make suitable changes to suit their needs.

Linking personality traits and stress responses in big cats

Glucocorticoids can serve as mediators of personality while animals develop coping style strategies (Carere *et al* 2010; Koolhaas *et al* 2010). For example, when an animal is faced with a challenge, its coping style is expressed through its personality as dictated by changes in glucocorticoid levels (Koolhaas *et al* 1999; Coppens *et al* 2010). Across different animal species, research shows that many proactive or bold individuals have low HPA-axis activity with lower glucocorticoid levels, while reactive or shy individuals have higher HPA-axis activity with higher glucocorticoid levels (Koolhaas *et al* 1999; Ellis *et al* 2006). Cheetahs rated by their keepers as 'nervous' types, for example, showed higher levels of glucocorticoids as compared to 'calm' types (Jurke *et al* 1997). In addition, clouded leopards that rated highly for fearfulness/tense, pacing, sleeping, self-injury or

https://doi.org/10.7120/09627286.31.1.009 Published online by Cambridge University Press

Figure 3

Factors that play a role in the relationship between personality and stress physiology.

hiding behaviours showed higher overall (base and peak) faecal glucocorticoid concentrations, indicating chronic stress (Wielebnowski *et al* 2002).

In a more recent study on captive African lions, social individuals had lower glucocorticoid levels compared to neurotic individuals that rated higher on the traits of being fearful of people, insecure, and tense (Torgerson-White & Bennett 2014). Similarly, in solitary felids like cheetahs, individuals that were rated sociable displayed lower glucocorticoid levels and were reproductively successful (Razal *et al* 2016). Thus, this crucial information is species-specific or individualistic and could be obtained by exploring personality and stress physiology. Lately, the literature consistently links big cat personality and stress physiology while indicating that there are some underlying factors that may influence this relationship.

Factors that may influence the relationship between personality and stress physiology

Multiple interlinked factors work together to influence the personality and stress physiology of big cats. Among these, the key factors commonly discussed across both personality and stress physiology literature are social interaction, environment, life history and evolutionary traits, genetics, and health (Figure 3). Though these factors have been comprehensively studied across different taxa, there is limited information available for some factors on big cats (Table 1; https://www.ufaw.org.uk/the-ufaw-journal/supplementary-material). Exploring these gaps will provide a better understanding of the individual responses of big cats living in captive or rescued environments.

Social interaction

The importance of social interaction and its role in shaping an animal's personality or stress physiology is emphasised in the past literature (Chadwick 2014). Social learning is a well-known concept in carnivores, where animals learn by observing their mothers, siblings or conspecifics (Sachser *et al* 2013). As cubs, felids spend considerable time with their mothers and these social interactions play a crucial part during their developmental stage, where social learning is maximised (Bertram 1975). Big cats in the wild, such as lions, live in a complex social group called a pride; in some instances male social groups have been observed in cheetahs while other conspecifics lead solitary lives as adults (Bertram 1975).

Big cats in captivity may be placed in abnormal social groupings with related or unrelated individuals due to restricted spacing. These forced social groupings may influence an animal positively to cope and develop better life skills, or negatively to be fearful of their conspecifics (Kaiser *et al* 2015). Any social interactions arising from captivity can affect an animal's behaviour and personality (Zayan 1991). When similar-aged female cheetahs were housed socially under similar environmental conditions, each individual's personality enabled them to develop their coping style to overcome social stress (Jurke *et al* 1997).

Social interaction also involves interaction between potential mates. Between a pair of tigers, the female displayed playful behaviours towards her male companion indicating positive social interaction (Bertocchi *et al* 2015). There have also been instances of mixed social interaction depending on the type of conspecific. For example, frequent

affiliative behaviours with few instances of aggression were observed among group-housed male cheetahs, and related males and females spent more time together in proximity and showed more affiliative interactions than the unrelated grouped individuals (Chadwick 2014). Additionally, when captive animals are closely placed near conspecifics of different species, the positive or negative interactions may influence their stress physiology. For example, when clouded leopards were placed near potential large predators, such as tigers, lions and leopards, they had higher faecal corticoid levels (Wielebnowski *et al* 2002). However, among a pair of captive tigers, although there was a tendency for the female to avoid the male during certain times, which could potentially represent a stressful behaviour, there was no variation seen in glucocorticoid levels (Bertocchi *et al* 2015). This variation could also be due to the low sample size.

Captive big cats, such as tigers, also frequently come in contact with humans through keeper interactions and sometimes through visitor interactions. While understanding the level of sociability, each tiger showed distinct personalities with varying levels of intraspecific sociality towards each other, whilst showing interspecific affiliative behaviours towards their keepers (Pastorino *et al* 2017). Similarly, friendly or aggressive personality traits towards their keepers were observed in lions (Torgerson-White & Bennett 2014). This varies among species and individuals. For example, the effects of keepers' social interactions on captive leopards in Indian zoos showed significantly lower glucocorticoid levels when handled by keepers with a positive attitude (Vaz *et al* 2017). However, for clouded leopards, there was no difference in glucocorticoid levels between individuals hand-reared by keepers versus mother-reared (Wielebnowski *et al* 2002).

Overall, social interactions with conspecifics, parents, siblings, or keepers are quite complex, and past research has contributed towards understanding its influence on the personality and stress physiology of big cats.

Environment

Many personality studies have focused on inter-species comparison while recognising environmental effects, because of the similar responses seen among wild cats (Gartner *et al* 2014), birds (Groothuis & Carere 2005) and humans (Gosling & Mehta 2013). Temporal and spatial changes in an animal's environment may bring about variations in its behavioural and physiological responses. While animals are mostly consistent in their responses to coping with environmental challenges, any environmental change such as adverse weather conditions, habitat loss, food scarcity, translocation or anthropogenic intervention require animals to cope and adapt (Clark & Ehlinger 1987; Van Buskirk 2012). The captive environment may involve several additional stressors; these include translocation into confinement with an artificial light, artificial substrate and unfamiliar odours which inhibit natural behaviours (Morgan & Tromborg 2007). However, when individuals are faced with a similar challenging situation again, they develop strategies that may become part of their coping style and behaviours (Bolger 1990). This was the case in captive Asiatic lions, as evidenced by bold, captive-raised individuals using the enclosure space more homogenously compared to shy and wild-rescued animals (Goswami *et al* 2020).

Research has focused on the physiological responses of big cats concerning their environment or any environmental changes. There was a significant negative association between enclosure height and faecal corticoids in clouded leopards, indicating the benefits of a higher minimum enclosure height (Wielebnowski *et al* 2002). Similarly, enclosure renovation led to changes in corticosterone levels before, during, and after habitat renovation for two out of six captive African lions (Torgerson-White & Bennett 2014). In the same study, the more vocal lions had higher baseline glucocorticoid values and high glucocorticoid levels during construction work (Torgerson-White & Bennett 2014). Among smaller wild cats such as jungle cats (*Felis chaus*), glucocorticoid levels were significantly higher for individuals living in smaller artificial enclosures without any hide-outs, thereby revealing the impact of the environment in shaping behavioural and physiological correlates (Marinath *et al* 2019). These variations imply that the individual welfare of big cats could be improved by considering their personality and monitoring their glucocorticoid levels while making changes in their environment.

Life-history and evolutionary traits

Though life-history traits are measured for populations and not for individuals, the variance in observed life-history traits is the product of selection acting on individual organisms (Stearns 1976). An individual's life history can be defined as the occurrence of events related to growth, survival and reproduction from birth to death (Bednekoff 2010). An animal's personality is closely linked to individual life-history traits, survival, and fitness; with direct links that bold individuals have a greater reproductive success. Similarly, while considering big cats for conservation breeding programmes, research on their personality can highlight certain indicative traits in individuals, such as extremely stressed or shy, to facilitate a positive welfare outcome. For example, fecundity in captive cheetahs was predicted by 'tense-fearful' personality traits and understanding this contributed new insights towards solving conservation breeding problems (Wielebnowski 1999).

Certain personality traits, such as exploratory behaviours, aggressiveness, boldness are necessary for survival in a wild population (Stamps 2007; Wolf *et al* 2007). Thus, specific life-history and evolutionary traits may predispose some felid species to be more prone to experience certain stressors in captivity. For example, female clouded leopards were smaller in size and show increased vigilance than males (Wielebnowski *et al* 2002). The authors suggest that females could have evolved with more vigilant personality traits due to their vulnerability to predators and also intersexual aggression or infanticide by males (Wielebnowski *et al* 2002). Thus, predation pressure in the smaller of the large-sized cats, such as cheetah and clouded leopard, may

https://doi.org/10.7120/09627286.31.1.009 Published online by Cambridge University Press

make them more prone to increased vigilance, hiding and escape behaviours, and may make them generally less suitable as an exhibit species. Moreover, while comparing personality traits with rearing history in captive Asiatic lions, behavioural diversity was observed to be significantly higher in captive-raised and bold lions compared to wild-rescued and shy individuals (Goswami *et al* 2020).

Under unfavourable conditions, the stress hormones can lead the animal to enter the emergency life-history stage to ensure survival and allow adaptation in their life (Moberg 2000; Wingfield *et al* 2015). The emergency life-history stage may force the animal to behave differently from their normal behaviours. This was evident in the case of birds where the effects of stress on the emergency life-history stage included redirection from normal behaviour to increased foraging or lower reproductive success rates (Moberg 1985; Wingfield *et al* 2015). In a similar case of captive cheetahs, cortisol levels among reproducing females were lower than the non-reproducing females after a restraint experiment (Jurke *et al* 1997). These findings suggest that stress can suppress major life-history strategies that then affect an individual's coping style.

An animal may develop life-history strategies to cope with a stressor, but other factors such as the age at which an individual is exposed to a stressor can also influence the life-history strategy (Monaghan & Haussmann 2015). Thus, understanding the influence of life-history traits on the personality and stress physiology of big cats may require long-term research (Clutton-Brock & Sheldon 2010). The findings may help to answer questions related to acute or chronic stressors impacting the welfare of captive and rescued big cats.

Genetics

Genes can influence both the personality traits and glucocorticoid levels of an individual (van Oers *et al* 2005). Genes related to personality traits can be identified using genome-wide approaches of quantitative trait locus (QTL) mapping or association studies (van Oers & Mueller 2010). The QTL research on animal personality has been limited to rodents and farm animals because one can obtain very specific selection lines to obtain suitable genetic strains (Andersson *et al* 1994; Gershenfeld *et al* 1997). In the case of wild animals, such as big cats, the genomes have been studied in detail to identify genotypes in tigers, lions and snow leopards (Cho *et al* 2013). Though it is difficult to manipulate crossing of desired genotypes, understanding the genetic make-up of big cats can reveal the historical pathway, provide information on genetic diversity, and help explore gene-environment interactions (Allendorf *et al* 2010; van Oers & Mueller 2010). To enhance the reproductive success for big cats in conservation breeding programmes, personality assessments could be useful for suggesting behaviourally compatible breeding pairs along with the genetic analysis to maintain diversity (Tetley & O'Hara 2012).

Genes also pass hereditary material which may have effects across several generations of evolution (Braastad 1998). For example, clouded leopards had high individual variations in faecal glucocorticoid levels, which may relate to the inherent variability of an individual's ability to cope in captivity (Zayan 1991; Carlstead & Shepherdson 2000; Wielebnowski *et al* 2002). To date, little evidence has been found between the influence of genes on the personality and stress physiology of big cats. Undertaking future genetic studies and linking them to individual responses could provide information on how individuals develop their coping styles to respond to stressors. This information may also be useful in identifying genotypes viable for breeding in captivity.

Health

Some animals are resilient to diseases whereas others are not (Cavigelli 2005). Variation in susceptibility may be due to the link between personality, stress and health (Friedman 1990, 2008; Cavigelli 2005; Sapolsky 2005). Addressing the health issues by looking at an animal's personality can provide improved health outcomes. However, the mechanisms linking animal personality to health remain inadequately understood in big cats but have been researched in other mammals. For example, neuroticism in primates can negatively influence the health of some animals leading to mortality (Deary *et al* 2010; Capitanio 2011; Gartner *et al* 2016). Thus, monitoring the neurotic individuals and tailoring to their needs by providing them with a less-stressful environment could help in recovery. Clouded leopards that were rated higher for agreeableness/openness, which are considered the opposite to neurotic personalities, showed higher levels of individual well-being (Gartner *et al* 2016).

Negative health consequences might arise if an animal cannot adapt or cope with the stressor (Koolhaas *et al* 1999). Stressful life events in the early years can pose some risk factors for development as adults. Earlier research on the personalities of endangered big cats has been beneficial for estimating their health status and in future can contribute towards monitoring health and identifying illnesses in early stages (Wielebnowski 1999; Gartner & Weiss 2013; Wang *et al* 2019).

Big cats in captivity may have lower disease resistance with a weak immune system (Wielebnowski *et al* 2002; Clubb & Mason 2003; Morgan & Tromborg 2007). For example, captive cheetahs have higher faecal corticoid levels than free-ranging cheetahs, suggesting that chronic stress may contribute to many captive cheetah health problems (Terio *et al* 2004). Thus, the HPA axis, which modulates the degree of adaption to stressors, can be in a continuous state of chronic stress if the animal is suffering (Maniam *et al* 2014).

Feline Immunodeficiency Virus (FIV) weakens the immune system of big cats making them susceptible to infections (Brown *et al* 1993). There are also instances of gastroenteritis in cheetahs and tigers associated with stress in captivity (Cociu *et al* 1974; Terio & Munson 2000; Wielebnowski *et al* 2002). These responses have important implications for assessing and maintaining the health and immunity of big cats and can help in providing tailored care for animals undergoing medical treatment (Narayan *et al* 2017).

Limitations and recommendations from big cat personality and stress physiology

Charismatic big cats often garner a lot of the attention in conservation, yet there is very limited focus on understanding their individual responses for welfare (Parnell *et al* 2014). Besides social interaction, environment, life-history and evolutionary traits, genetics, and health influencing their welfare; other factors such as animal's age, reproductive status, sex, body condition, diet, and seasonal variation may also lead to a variation in data collection (Touma *et al* 2003; Bertocchi *et al* 2015). Though it might be difficult to control all the factors, trying to recognise and addressing some of them during the research planning could help to address some of the limitations. For example, accessing secondary data maintained by international accredited zoos such as Zoological Information Management System (ZIMS) would be useful in providing a detailed history of big cats. More robust results may be obtained if studies are carried out on a long-term basis, although this may not always be feasible. Lastly, there are certainly many opportunities for further research that could be carried out with reasonable sample sizes, especially if the research is multi-institutional in nature.

Limitations and recommendations from Personality Studies

Researching the personality of big cats has gained attention only recently. Keepers' attitudes can play an important role in promoting an animal's well-being. Literature on other species, such as captive black rhinoceros (*Diceros bicornis*), Chapman's zebra (*Equus burchellii*) and Sulawesi crested black macaques (*Macaca nigra*) shows unique keeper-animal dyads formed due to the keepers' 'attitude towards the animals' and their 'knowledge and experience of the animals' (Ward & Melfi 2015). However, these interactions may change as different keepers with different personalities take care of animals over their lifetimes (Phillips *et al* 2017). Some common limitations of this approach include the time spent observing an animal to understand its behaviour and personality. Due to daily husbandry routines, keepers that work with multiple animals get to spend limited time with their big cats. Sometimes, though the keepers may be working with a big cat for many years, they may not have an opportunity to observe their animal's behaviours throughout the day (Phillips *et al* 2017). Researchers, on the other hand, may spend more time observing animal behaviours and may also be able to rate the personality of the animals (Phillips & Peck 2007; Phillips *et al* 2017). When different keepers or researchers are asked to rate the same big cat, testing the inter-observer reliability of raters will help avoid discrepancies between them.

Limitations and recommendations from Stress Physiology Studies

The field of stress physiology is constantly progressing towards non-invasive techniques for assessing stress levels. In recent years, there has been a more standardised approach to the use of faecal samples as opposed to urine, blood or saliva in big cats (Young *et al* 2004; Palme *et al* 2005; Conforti *et al* 2012; Sgambelluri 2018). However, one limitation here would be that faecal samples are very opportunistic because cats can be secretive in defaecating. Secondly, different countries have different policies for working with wild animals. Hence, methods such as using artificial dyes to identify individual faecal samples among social animals, are considered invasive in countries where big cats are endangered (Wielebnowski & Watters 2007).

Further, commercial hormone kits are expensive and quick to expire. Hence, over the years, researchers have developed their own EIA/RIA and a validation of these methods is beneficial to overcome this limitation. This could also be one of the major reasons for variation in results, raising the challenge of comparing the results across felids, but working towards standardisation of these techniques could benefit wild big cat conservation (Bhattacharjee *et al* 2015; Pavlova *et al* 2015; Mesa-Cruz *et al* 2016).

Animal welfare implications and conclusion

Managing big cats more effectively in captivity relies on an understanding of the stressors they face and how different individuals respond to them. This review summarises research conducted on large felid personality and its connection to captive breeding and welfare over the past 33 years. It has identified five key factors: social interaction, environment, life-history and evolutionary traits, genetics, and health that could influence the personality of the big cat along with stressors. The first two factors have been extensively studied in the literature; however, the last three are potentially very promising avenues for future research through integrated approaches.

There is a need to explore these factors and how they play a role in shaping captive big cats' personality. As many captive big cats are part of conservation breeding programmes, future studies integrating personality and stress physiology can advance our understanding of human-animal interactions, facilitate better husbandry, inform the development of more effective welfare and management policies, boost conservation outcomes and assist with reintroduction programmes. After acquiring better knowledge about how certain personalities cope with stressors, we can make changes in the environment to suit their needs to benefit the overall welfare of big cats.

Declaration of interest

The authors declare no conflict of interest.

Acknowledgements

We thank Stephanie Hing, Susan Mowbray, Shamim Aryampa, Corinne Letendre and John Hunt for their valuable comments on the manuscript and Gary Dennis, and Alana Bartley for useful discussions.

https://doi.org/10.7120/09627286.31.1.009 Published online by Cambridge University Press

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