WESTERN SYDNEY
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Application of interdisciplinary approaches to improve the welfare of big cats

by

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MSc., Wildlife Biology

A thesis submitted in fulfilment of
the requirements for the degree of
Doctor of Philosophy

School of Science

Western Sydney University

July 2022

"Only if we understand, will we care. Only if we care, will we help.

Only if we help shall all be saved"

— Jane Goodall

Acknowledgements

I respectfully acknowledge the *Darug* people as the traditional custodians of the land on which I lived and worked during my PhD.

A PhD is like a child, and it takes a village to raise this 'PhD child'

I am extremely thankful to my primary supervisor Prof. John Hunt for the entirety of my PhD candidature and for the liberty to explore the topic in my own way while constantly providing guidance and advice. Your patience in teaching me stats and down-to-earth attitude has been a turning point in my professional life. I am especially indebted to Prof. Gary Dennis for being my silent supporter and mentor. I am grateful for the additional guidance from my collaborator Dr Vidya Athreya in developing one of the challenging research projects remotely. I am also thankful to Dr Edward Narayan, Dr Stephanie Hing, Dr Alan McElligott and Dr Clarissa House for sharing their expertise on the preliminary ideas of the research projects and contributions to the research.

Without the financial and material support from the Australia Awards (Endeavour Leadership Program) and the School of Science at Western Sydney University, this thesis would never have been written. The professional training workshops especially those conducted by Dr Susan Mowbray and Dr Russell Thompson, and the critical feedback provided by them on my drafts helped me enhance my skills. Special thanks to my counsellor at WSU, who has been my cheerleader and helped me get through my candidature especially on my worst days. I simply could not have made it to the finish line of my marathon without your support!

As a fieldwork-based study, this thesis relied on the cooperation of big cat managers, stakeholders and other local participants. My sincere thanks go to the staff at Zambi Wildlife Retreat (Donna, Tara, Brooke), Sydney Zoo (David, Sam, Amanda, Simon), Sanjay Gandhi National Park Forest Department (Mr. Limaye (P.C.C.F.) and team) and the other respondents who contributed to this research. I wish to thank my dedicated volunteers – Alana Bartley and Mrunal Ghosalkar for all your efforts in data collection and valuable discussions about the projects. Many thanks to Mark Emanuel for his assistance in the laboratory and for always providing me with all the resources I needed.

Being away from home and pursuing a PhD during a global pandemic was one of the most difficult tasks. To the friends and roommates I made during my candidature - Corinne, Kristen, Andrea, Shamim, Sharon, Fiona, Julia, Sunayana, Mahmuda, Victoria, it has been so wonderful to have your support while taking a similar path and I am indebted for all the brainstorming sessions which made my thoughts clearer. Thank you for best the company during the lunchtimes, zoom calls, bushwalks, doctor appointments, and I will always cherish our friendship. I was also surrounded by

wonderful friends outside the university, who are now my Australian fam and who have been a part of my 'life's first-evers' - Le Poidevin family and Adley, thanks for always checking on me and making me feel at home. My beautiful Richmond town and friends – the singing group, the veggie barter group, the ukulele group, it was not limited only there, I am so so grateful that you have fed and ate with me, laughed with and at me and most importantly, listened to me.

I was fortunate to meet my industry mentor Heather Catchpole through the industry mentoring program called IMNIS, who positively encouraged me to continue pursuing my passion and helped me build professional networks. I am also very lucky to have great mentors in the past –Baskaran sir, Smita ma'am, Pushpa ma'am, Conrad sir, Sujata ma'am, Madhuri ma'am, Goldin sir, Fr Savio, Radhika ma'am and many others I have worked with in India, without their support I would not be here today.

To my friends back home in India –Nikit, Orvill, Senan, Stephen, Tejas who jumped on zoom calls to help me with my PhD work and also heard my PhD hardship rants- Thank you always! Also, Delfi for teaching me the ABC's of studying and understanding human perceptions.

I wish to say a special thank you to all my family for their continued patience and support while I have studied. To my dad, mom, brother, aunts, uncles and cousins for believing in me and encouraging me to do what I love, even though it was out of your scope, and for not letting your hurdles be known or letting me worry. And a big thank you to my better half Wilber, for being with me in this roller-coaster of a project and for making this a part of your dream too. I could not have done this without your love, understanding and encouragement. This thesis is dedicated to you and my family.

Finally, to my precious cats back home - Mushy, Zumi and Cloudy, who gave me this inspiration to take to the world that each of you are unique. No matter what this thesis says, but you are the best inspiration!

Statement of Authentication

I declare that the work presented in this thesis is original, except as acknowledged in the text, to the best of my knowledge and belief.

I certify that I have not submitted this material in part or full for a degree at this institution or another.

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Janice Vaz

July 2022

COVID-19 Impact Statement

Due to the impact of COVID-19 restrictions, various amendments have been made to this research. Firstly, due to the nature of the studies being field based for Chapter 3 and 4, even though we received permission to conduct the research in various zoos across Australia, we were only able to conduct it in the zoos in NSW. With regards to surveying participants in India for Chapter 6, the original intention was to conduct interviews in the field with participants. Unfortunately, we had to opt for online semi-structured interviews due to which some of the stakeholder groups could not be included. This resulted in a smaller number of participants being recruited than initially intended. A substantial amount of time and effort also went into amending the ethics approvals to request changes in the modes of data collection and in designing new studies.

Author's Declarations

The research contributing to this thesis was conducted by Janice Vaz (JV) who was a recipient of the Australia Awards - Endeavour Leadership Program. JV was also supported through the Higher Degree Research Training Program funds allocated by the School of Science from Western Sydney University. This thesis is presented as a series of discrete manuscripts that were drafted by JV with comments from John Hunt (JH), and Vidya Athreya (VA) and other external experts. In addition, a few others have contributed to each chapter.

Chapter Two

JV, Edward Narayan (EN), Alan G McElligott (AGM) conceived the ideas and designed the chapter. JV wrote the chapter, with comments and editing from EN and AGM. A version of this chapter has been published in *Animal Welfare.*

Citation: Vaz, J, McElligott, AG, Narayan, E. (2022). Linking the roles of personality and stress physiology for managing the welfare of captive big cats. *Animal Welfare.* 31 (1): 99-111(13).

Chapter Three

JV and JH conceived the ideas and designed the methodology, with input from EN and AGM. JV and Alana Bartley (AB) collected the data. JV analysed the data with the help of JH. JV wrote the manuscript with comments and editing from JH. A version of this chapter has been published in *BMC Zoology*.

Citation: Vaz, J., Bartley, A. & Hunt, J. (2022). Personality matters: exploring the relationship between personality and stress physiology in captive African lions. *BMC Zoology* 7, 30. https://doi.org/10.1186/s40850-022-00126-9

Chapter Four

JV and JH conceived the ideas and designed the methodology. JV and AB collected the data. JV analysed the data with the help of JH. JV wrote the manuscript with comments and editing from JH.

Potential journal for publication: Frontiers in Zoology

Chapter Five

JV and JH conceived the ideas and designed the methodology. JV collected the data. JV analysed the data with the help of JH. JV wrote the manuscript with comments and editing from JH.

Potential journal for publication: Journal of Applied Animal Welfare Science

Chapter Six

JV, VA and JH conceived the ideas and designed the methodology. JV and Mrunal Ghosalkar (MG) collected the data. JV analysed the data with the help of JH and VA. JV wrote the manuscript with comments and editing from VA and JH.

Potential journals for publication: People and Nature (British Ecological society), Frontiers in Conservation Science

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List of Abbreviations

ACG	Aarey Conservation Group
ACTH	Adrenocorticotropic Hormone
AI	Association Index
BNHS	Bombay Natural History Society
CA	Catecholamines
CSG	Civil Society Group
CVA	Canonical Variate Analysis
CZA	Central Zoo Authority
CSR	Corporate Social Responsibility
DFA	Discriminant Function Analysis
EI	Electivity Index
EIA	Enzyme immunoassay
FDM	Five Domains Model
FFM	Five Factor Model
GC	Glucocorticoids
GLM	General Linear Model
HLI	Human-Leopard Interactions
HPA	Hypothalamo–Pituitary–Adrenal
ICC	Intra-class Correlation Coefficients
IRT	Infrared Thermography
IUCN	International Union for Conservation of Nature
MfSGNP	Mumbaikars for SGNP
NGO	Non-Governmental Organisation
OCEAN	Openness to experience, conscientiousness, extraversion, agreeableness, and neuroticism

PARTNERS	Presence, Aptness, Respect, Transparency, Negotiation, Empathy, Responsiveness and Strategic Support
PAW	Positive Animal Welfare
PCA	Principal Component Analysis
RAWW	Resqink Association for Wildlife Welfare
SAM	Sympathetic-adrenomedullary
SGNP	Sanjay Gandhi National Park
SPI	Spread of Participation Index
SZ	Sydney Zoo
UBCG	Urban Biodiversity Conservation Group
WWF	World Wide Fund for Nature
ZAA	Zoo and Aquarium Association
ZIMS	Zoological Information Management Software
ZWR	Zambi Wildlife Retreat

Abstract

For many years, the study of animals and of humans were considered as two different realms with each having little to no relevance to the other. Theories and standardised methods from the natural sciences were objectively applied to all animal species to solve problems. However, just like humans, individual animals may respond differently to different situations or stressors. Looking at all animals through a 'one size fits all' lens was recognised as ineffective and the importance of observing animals directly, using welfare indicators and implementing policies to safeguard their welfare evolved. Animal welfare science began by exploring the needs of farm and pet animals and slowly expanded to include wild animals, both in captivity and the wild. Animal welfare is now recognised as a multifaceted concept. It acknowledges animals need to express their natural behaviours and it encompasses an animal's physical and psychological well-being. It is important to note that levels of animal welfare largely depend on the society and the attitudes of humans within it. In recent years a fascination towards charismatic big cats has increased, largely due to the media and streaming services. At the same time, threats such as poaching, entertainment, human development and conflicts are rising which may affect their welfare.

The ongoing nature of many of these threats continues to compromise the welfare of big cats. It is therefore essential to address these concerns to ensure the well-being and ongoing welfare of big cats. In the last few years, advancements in the field of animal welfare show that understanding individual variations in animals can play a key role in improving their welfare. In the case of farm animals, learning about their sentience has prompted better management policies. Similarly, awareness about individual big cats and their needs can help to improve their welfare, both individually and overall. Research increasingly shows that variations in behaviour may indicate personality and variations in GC hormones may be indicative of a big cat's coping capacity. By integrating variations in behaviour with an animal's physiology, any internal and external changes in the animal may be highlighted. Likewise, exploring

people's attitudes toward big cat welfare may provide insights to inform decision making and/or actions towards big cats.

This research, across five studies, examines the effectiveness of broad interdisciplinary approaches from the fields of natural and social sciences to assess big cat welfare. It first reviews the research on the role of individual variation in understanding the relationship between personality and stress physiology in big cats. In reviewing the past literature on big cat personality and stress physiology, we compared the methods used and identified five factors - social interactions, environment, life history and evolutionary traits, genetics, and health, that may influence this integrated relationship. We then applied these inferences to explore personality in captive Twenty-two African lions (13 males and 9 females). This involved using a wild cat personality checklist with 52 feline traits rated by cartetakers and researchers (n=5) and comparing it with the cats' faecal cortisol levels. A strong correlation was found between lion personality and cortisol levels, where African lions with agreeable personality types had lower cortisol levels. Next, we examined social and environmental factors identified as influencing factors in the review and measured it using the association index, the spread of participation index and electivity index in these captive African lions (n=22). These three indices were then compared with the lion's personality, cortisol levels, enclosure size and age, to determine the driving factors affecting social and environmental preferences. The social interactions in African lions were negatively influenced by dominant personality types and lions rated higher on agreeableness showed some tendency to use secluded shaded areas with enrichments to remove themselves. While previous study focused on understanding the individual animal's welfare by observing animals directly, this time we analysed the role of human attitudes towards big cat welfare. We assessed the attitudes of the general public (n=375) towards captive big cats in India and Australia via an online survey and identified the demographic factors influencing their attitudes and found that the number of zoo visits is a common factor influencing people's perspectives of captive big cats and their welfare, with factors such as location, age, gender and education, and some of their interactions, also influencing several parameters. Finally, we assessed the attitudes of thirty-five stakeholders

towards wild leopards in the Sanjay Gandhi National Park, India using an online survey followed by a semi-structured. We examined if these perceptions varied with their role but found that there was no difference in the perceptions of the seven stakeholder groups towards leopards as an issue, in threats towards leopards in the Sanjay Gandhi National Park as part of the urban landscape of Mumbai, and factors resulting in the reduction of leopard attacks.

These interdisciplinary studies demonstrate the effectiveness of using integrated approaches to assess the coping capacity of individual animals. They have also illuminated the role of human attitudes in more widely and effectively promoting big cat welfare. This research identifies welfare indicators using methods from across multiple disciplines to develop strategies to first, enhance the welfare of big cats in managed environments and second, encourage animal welfare advocacy and actions through providing deeper understandings of human perceptions of big cats. This research provides novel evidence that interdisciplinary approaches to assessing animal welfare such as animal personality, stress physiology and human attitudes are useful to improving the welfare of big cats.

Chapter 1: Introduction

The introductory chapter provides an overview of animal welfare, specifically factors affecting the welfare of big cats in captivity and the wild. The concept of animal welfare is complex and often requires interdisciplinary approaches to help improve outcomes for animals. This chapter explains the significance of animal personality, stress physiology and human's perception to big cat welfare. The chapter then details the main research questions guiding this research and concludes by outlining the scope and limitations of the research and the structure of the thesis which is presented as a series of papers.

1.1 Overview of animal welfare: Moving towards positive animal welfare from a traditional welfare approach

In the mid-1960s, concerns around animal welfare and the well-being of farm animals began (Brambell, 1965; Harrison, 1964). These concerns highlighted the need to consider both the physical and mental needs of animals, such as allowing them to express normal behaviours without fear and/or distress. Further intensive research in this area raised more interest. This led to the creation of the *Five Freedoms* that provide a comprehensive approach to considering animals' welfare state (FAWC, 1979a). They include, for example, at all times treating an animal - whether on a farm, in transit, at a market, in a slaughterhouse, zoo, rescue centre or in the wild – in line with the *Five Freedoms*. The *Five Freedoms* were amended in 1993, and have ever since served as the foundation for improving animal welfare standards through evidence-based scientific research (FAWC, 1993) (Table 1.1).

Table 1. 1 Five Freedoms of Animal Welfare and Five Domains of Animal Welfare

Five Freedoms of Animal Welfare	**Five Domains of Animal Welfare**
Freedom from hunger and thirst	Nutrition
Freedom from discomfort	Environment
Freedom from pain, injury, or disease	Health
Freedom to express normal behaviour	Behaviour
Freedom from fear and distress	Mental state

By 1994, studies began recognising that animals can experience feelings, ranging from negative to positive; these understandings further developed *The Five Domains Model* (FDM) (Mellor et al., 2020; Mellor & Reid, 1994). The FDM consists of the domains of nutrition, environment, health, behaviour, and mental state (Mellor, 2017). The first four domains (nutrition, environment, health, and behaviour) all contribute to understanding the animal's experiences and make up the fifth domain, the mental domain. Thus, the Five Freedoms and the FDM are guiding principles to assess an animal's welfare overall.

More recently, animal sentience has been accepted, making animals similar to humans when they feel stressed or express emotions. This understanding encouraged a big shift in attitudes, from satisfying an animal's basic "needs" to considering an animal's "wants" or "preferences"; this signalled the move from a traditional animal welfare approach to a more positive animal welfare approach (PAW) (Fraser & Duncan, 1998; Yeates & Main, 2008) (Figure 1.1). PAW recognizes and considers an animal's emotional well-being and encompasses four features. These are positive emotions, positive affective engagement, quality of life, and happiness; these factors are now acknowledged alongside the Five Domains of traditional animal welfare (Lawrence, Vigors, & Sandøe, 2019). There is also increasing evidence to support the usefulness of PAW in pets and farm animals (Boissy & Erhard, 2014; Morton, 2007). Indicators vary according to the species however, and there is an increasing urgency to apply it to endangered animals like big cats.

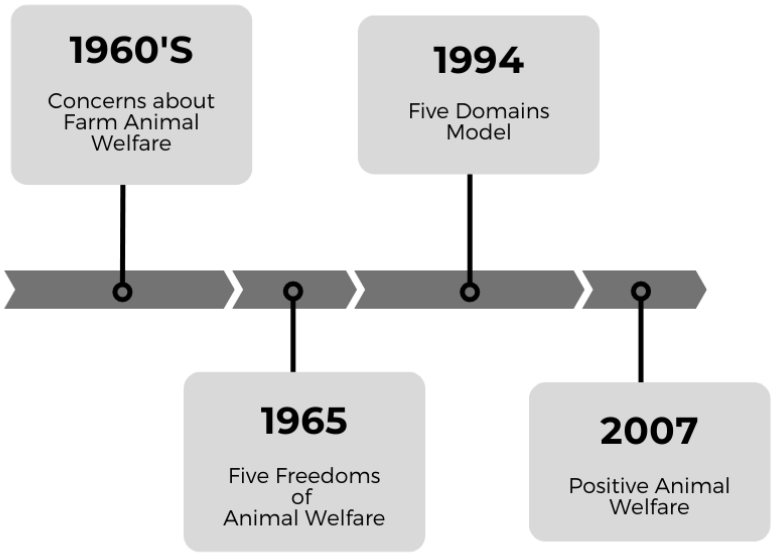

Figure 1. 1 Major changes to the field of animal welfare over the years

1.2 Big cat welfare – captivity and wild

Big cats refer to felids 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 *Neofelis nebulosa*) and large sized cats of the subfamily *Felinae* (such as cheetah *Acinonyx jubatus*, puma/cougar *Puma concolor* and lynx *Lynx canadensis*). Big cats live in vast habitats in the wild, and due to their declining numbers, the International Union for Conservation of Nature (IUCN) RedList lists many species of big cats as endangered or vulnerable (Bauer, Packer, Funston, Henschel, & Nowell, 2016; Goodrich et al., 2015; Stein et al., 2016). Big cats are also managed under human care in zoos, circuses, reintroduction programs and rescue centres. When managing big cats, general animal welfare standards are adapted to suit the needs of the big cats using standard husbandry protocols.

The general animal welfare standards include guidelines for carnivores which are set by regional zoological regulators such as the Zoo and Aquarium Association (ZAA)

in Australia and Central Zoo Authority (CZA) in India. These guidelines are adapted from the World Association of Zoos and Aquariums standards based on years of research on the species (Lion Care Manual, 2012). The welfare standards thus vary depending on the management team and how long the setup of the zoo has been in place. For example, newer zoological parks are designed to let most big cats move freely in a more naturalistic enclosure without cages. Thus, different welfare outcomes are often seen among different facilities managing big cats while trying to meet the same animal welfare requirements (Cole & Fraser, 2018). However, the 'one size fits all' welfare strategy of looking at animals from a species view may not promote the best welfare outcome for every individual (Wolfensohn et al., 2018). The welfare indicators thus also vary between individual big cats, and animal personality is recognized as a key factor contributing to this variation (Finkemeier, Langbein, & Puppe, 2018; G. J. Mason & Mendl, 1993).

1.3 Welfare and personality in big cats

In the last few decades there has been a tremendous increase in looking at animals as individuals and not as species, with an emphasis on recognizing an animal's personality (Boissy & Erhard, 2014; Finkemeier et al., 2018; Koolhaas, 2008). Personality is defined as individual behavioural differences in an individual's life that are consistent across time and situations (Budaev, Zworykin, & Mochek, 1999; Finkemeier et al., 2018; Gosling, 2008; Koolhaas et al., 1999; Réale, Reader, Sol, McDougall, & Dingemanse, 2007). Studies on animal personality first emerged from human studies and were later applied to non-human primates (H. D. Freeman & Gosling, 2010). Over the years, researchers have argued about the noticeable differences observed among animals. This led to researchers exploring the personalities of various species such as domestic (Ilska et al., 2017; Litchfield et al., 2017), farm (Finkemeier et al., 2018; van Erp-van der Kooij et al., 2003) and other wild animals (Clary et al., 2014; Groothuis & Carere, 2005; Pastorino, Christodoulides, et al.,

2017). These studies have documented behaviours among various individuals in a species and these have been adapted to inform and develop customized personality checklists.

Among felids, the personality of domestic cats is the most studied (*Felis silvestris catus*). More recently, the personality of wild and captive felids such as snow leopards (*Panthera uncia*; (Gartner & Powell, 2012)), cheetahs (*Acinonyx jubatus*; (Wielebnowski, 1999)), clouded leopards (*Neofelis nebulosa*; (Wielebnowski, Fletchall, Carlstead, Busso, & Brown, 2002)), tigers (*Panthera tigris tigris*; (Pastorino, Paini, Williams, Faustini, & Mazzola, 2017; Phillips & Peck, 2007)) and lions (*Panthera leo*; (Torgerson-White & Bennett, 2014)), (*Panthera leo persica*; (Quintavalle Pastorino et al., 2017)) have also been considered (Vaz, McElligott, & Narayan, 2022). As many species of big cats live elusive lives which may be solitary or social, this makes it complex to understand their behaviours. However, understanding the behaviours of individual big cats is crucial to promote their survival and well-being.

Previously, individual differences in big cats' behaviours were considered to be background noise or outliers as individuals who behaved differently could not be compared to other animals who were assigned certain categories of behaviour. However, many animals fall in the middle of categories of behaviours or show a variation in personality depending on their coping or adaptive capacity. Gartner, Powell, and Weiss (2014), for example, found different personality types among various wild cats. In fact, among related wild cats managed under the same environments, repeatable individual behavioural differences were observed (Lewejohann, Zipser, & Sachser, 2011; Müller & Müller, 2015). Thus, studies are now working to determine the causes, consequences and underlying mechanisms of these behavioural differences, which can be highly structured for an animal's survival (Wolf & Weissing, 2012). Specific personalities may reveal proxies for an individual's emotional states or psychological or physiological conditions, and/or may be determinants of an animal's fitness and welfare (Richter & Hintze, 2019). It is therefore

useful to understand these differences to assess individual welfare to improve overall welfare (Wolf & Weissing, 2010).

1.3.1 Measuring big cat personality

It is important to assess animal personalities using methods that can be replicated across individuals. Coding and rating are two methods commonly used to assess personality in animals (Gosling, 2001; Highfill, Hanbury, Kristiansen, Kuczaj, & Watson, 2010; Torgerson-White & Bennett, 2014). Coding involves recording behavioural frequency observations to develop behavioural time budgets and is further used to create personality axes. Ratings methods involves scoring traits on a checklist developed for wild cats (Highfill et al., 2010). In coding, since observations are made for a particular duration, the possibility of missing out on some of the data exists whereas, in rating, the score depends upon the observer's relationship with the animal, and it is challenging to rate animals reliably without imposing subjective views (Réale & Dingemanse, 2012). Both of these methods have strengths and limitations, and studies on big cats' personality have used both the coding (Boccacino, Maia, Santos, & Santori, 2018; Chadwick, 2014) and rating (Gartner et al., 2014; Phillips & Peck, 2007) methods.

More robust methods of rating are available. These include a comprehensive checklist developed for wild cats from other species (Gartner, 2013; Wielebnowski, 1999). An inter-observer reliability test involving more than one rater can also be followed to help avoid bias and promote consistency in monitoring animal behaviour (Phillips & Peck, 2007; Wielebnowski, 1999). Various reliability tests are available and selecting the appropriate measure helps in identifying the reliable behavioural traits (Koo & Li, 2016). For example, using the Intra-class Correlation Coefficients (ICC), the traits may be analysed using multivariate statistics such as Principal Component Analysis (PCA) or Canonical Variate Analysis (CVA) to reduce the behavioural traits to components (A. Carter & Feeney, 2012; Litchfield et al., 2017). These reduced

components may be further investigated to determine what feline personality dimension they fit. The feline personality dimensions can be chosen either by assessing the continuum of one personality dimension such as bold-shy (Goswami et al., 2020), or by assessing multiple dimensions using the Five Factor Model (Gartner et al., 2014; Litchfield et al., 2017). Based on the Five Factor Model (FFM), which is modified from human personality studies, the identified components of the PCA or CVA can be categorised into various personalities such as openness to experience, conscientiousness, extraversion, agreeableness, and neuroticism, abbreviated to OCEAN (Digman, 1990; Goldberg, 1992). These human personality dimensions were translated to suit feline behaviours to include dominance, which may not be very evident in humans (Gartner & Weiss, 2013a; King & Figueredo, 1997).

1.3.2 Challenges in studying big cat personality research

Other terminologies such as individual differences (Clark & Ehlinger, 1987), temperament (Réale et al., 2007), coping style (Koolhaas et al., 1999) and behavioural syndrome (Sih, Bell, & Johnson, 2004) have previously been frequently used as alternate definitions to personality (Réale et al., 2007). As stated, this understanding has since shifted and studies on big cat personality have increased in the past few years. However, varying methods of data collection such as differences in rating and coding methods, and analysis have led to inconsistencies in the literature (Mirkó, Dóka, & Miklósi, 2013). Other studies have introduced novel objects and then studied personality, which may impact the validity or outcome of empirical tests (M. I. Kaiser & Müller, 2021). In the wild, researchers face other challenges to study the personality or observe the behaviours of big cats due to their secretive lives across different environments.

1.4. Welfare and stress physiology in big cats

Stress responses have a significant role in allowing animals to cope with environmental challenges – for example, while facing a predator in the wild, a prey may experience stress and prepare to escape (Sheriff, Dantzer, Delehanty, Palme, & Boonstra, 2011). Such stressors can cause either acute or chronic stress responses which can have specific consequences for an animal's welfare, health or well-being. An animal's constant striving for adaptation during a potentially stressful incident is called allostasis (Sterling & Eyer, 1988), which is important for maintaining homeostasis. However, circumstances which overstimulate an animal's allostatic systems can lead to a condition termed "allostatic load"; this is also recognized as the price of adaptation (McEwen & Stellar, 1993).

Short exposure to stressors, such as a sudden loud sound, can lead to acute stress. Repeated or prolonged acute stressors, such as confinement, can lead to chronic stress (Moberg, 2000; Narayan, Willis, Thompson, Hunter-Ishikawa, & Bendixsen, 2018). While acute stress responses can allow animals to escape from threats and help achieve adaptation, chronic stress can affect the long-term immunity, health, behaviour and hence overall fitness of animals (Broom & Johnson, 1993; Hing, Narayan, Thompson, & Godfrey, 2016; Moberg, 2000; Sapolsky, Uno, Rebert, & Finch, 1990). These varying internal GC variations can also act as physiological indicators of welfare (Dantzer & Mormede, 1983; Dantzer, Mormède, Bluthé, & Soissons, 1983; Moberg, 1985). It is now understood that lower GC levels may not necessarily mean that an animal is in stress (M. J. Dickens & Romero, 2013). When used comparatively with other measures such as behaviour, GC levels may be a better indicator of an animal's welfare.

The potential of stress physiology to help assess animals' welfare has been extensively studied. The first published use of the word 'stress' in relation to animals was in 1987 in a study on cheetahs (Wildt et al., 1987). This was followed by studies on

other big cats (Wildt et al., 1988). It is now understood that when an animal is faced with a stressor or challenge, there is a non-specific internal stress response which activates two "stress axes" – the hypothalamo–pituitary–adrenal (HPA) and the sympathetic-adrenomedullary (SAM) of the nervous system which causes acute or chronic effects (Cannon, 1914; Selye, 1973) (Figure 1.2).

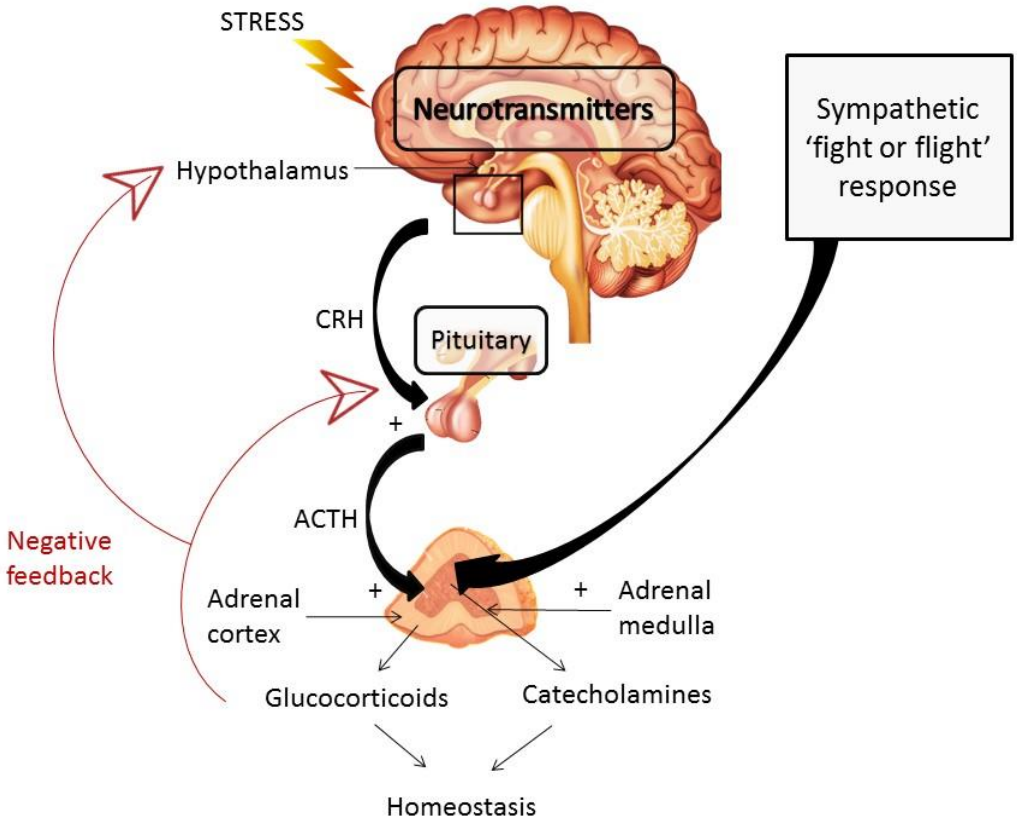

Figure 1. 2 Stress physiology in vertebrates. Schematic diagram of the HPA axis and SAM pathway when an external stimulus is perceived as a stressor modified from (Matteri, Carroll, & Dyer, 2000)

This HPA activation starts with the hypothalamus releasing corticotrophin-releasing hormone, which acts on the anterior pituitary to secrete adrenocorticotropic hormone (ACTH) (Oakley & Cidlowski, 2013). Furthermore, ACTH acts on the adrenal cortex to stimulate the production and secretion of glucocorticoids (Oakley & Cidlowski, 2013; Sapolsky, Romero, & Munck, 2000). The neurohormonal activation of

the sympathetic-adrenomedullary (SAM) system initiates the release of catecholamine from the adrenal medulla which operates under the flight-fight response. Glucocorticoids (GC) and catecholamines (CA) act on a variety of target tissues and organs to maintain homeostasis and thereby form the frontline responses to stressors in animals (Armario, 2015; Matteri et al., 2000). The GCs are then released and transported through the blood to reach the target organs. Among the GCs are the stress associated hormones – cortisol and corticosterone – which are secreted in varying quantities in different species. The SAM system secretes CAs – epinephrine and norepinephrine, within a fraction of seconds upon activation (Palme, Rettenbacher, Touma, El-Bahr, & MÖStl, 2005). In summary, when an animal faces a range of stressors or a change, their body initiates an internal neuroendocrine response involving the release of hormones called catecholamines (rapid flight-fight response) and glucocorticoids (slow responding endocrine response) with acute or chronic effects (Schneiderman, Ironson, & Siegel, 2005; Selye, 1973). As GCs remain in the body longer, they are usually studied over CAs. Glucocorticoids were first studied by invasive procedures where animals were culled to weigh their adrenals to study stress (Cannon, 1914). Later, this was achieved surgically via implanted infusion pumps to collect blood and plasma samples (J. L. Brown, Goodrowe, Simmons, Armstrong, & Wildt, 1988; Nogueira & Silva, 1997). Less invasive procedures using saliva, urine and faecal samples have since been developed (Palme et al., 2005; Sheriff et al., 2011). Recent advances in stress physiology are trending towards developing non-invasive techniques, where stress is studied by minimal direct contact with the animal and without exposing them to any additional stressors.

GCs are essential hormones that play a fundamental role in the body such as regulating circadian rhythm, energy regulation, reproduction, and immune function. GCs can fluctuate all the time for myriad reasons other than stress, hence 'GCs' and 'stress' are not synonymous and have other roles outside of the organismal stress response (MacDougall-Shackleton, Bonier, Romero, & Moore, 2019). However, when

combined with data exploring behaviour of an animal or perceived stressors in an environment, it can be extremely useful to understand and justify what the levels of GCs signify.

The GC levels vary between individual animals and many factors contribute to this variation (Cockrem, 2013b). These include genetic differences between animals along with pre- and post-natal adult experiences (Bonier, Martin, Moore, & Wingfield, 2009; Inoue-Murayama, Yokoyama, Yamanashi, & Weiss, 2018). Other factors that play a role in variations in individual animals' GC levels include age, sex, personality, body condition, time of year, stage of breeding and the environment (Anestis, Bribiescas, & Hasselschwert, 2006; Cockrem, 2013b; Fourie & Bernstein, 2011; McEwen & Stellar, 1993; Moberg, 1985; Scallet, Suomi, & Bowman, 1981). Individual responses to all stressors may also differ from the mean response in the same species. In the past, individual variation data were considered as statistical 'outliers' because they fell out of the normal mean range (T. D. Williams, 2008). However, there are benefits of having individual variation in stress physiology. What may be very stressful for one animal may not be for another individual (Carere, Caramaschi, & Fawcett, 2010). Therefore, individual variation in GCs can provide insights into the plasticity or flexibility animals show as they perceive different stressors.

1.4.1. Measuring glucocorticoids– Moving from traditional to non-invasive methods

1.4.1.1. Hormone analysis

GCs can be used as an indicator of an animal's physiological state.. These GCs can be obtained from blood (plasma or serum) (J. L. Brown et al., 1988; Nogueira & Silva, 1997), saliva (Sgambelluri, 2018), hair (Schildkraut, 2016), faeces (Vaz et al., 2017), urine (Carlstead, Brown, Monfort, Killens, & Wildt, 1992), feathers (Sheriff et al., 2011) or claws (Baxter-Gilbert, Riley, Mastromonaco, Litzgus, & Lesbarrères, 2014). Some methods can be invasive and increase GC levels in the animal, hence researchers are

moving towards non-invasive methods that can be more readily used even on free ranging animals (Palme et al., 2005). For the practicality of assessing the GC in felids, faecal metabolite assays are a better suited approach (Narayan, Baskaran, & Vaz, 2017; Narayan et al., 2013), but GCs do not directly provide a quantification of stress level (MacDougall-Shackleton et al., 2019). Other than faeces, hair is another non-invasive alternative to evaluate chronic stress in felids because it reflects physiological stress experienced by the animal over longer periods, from weeks to months (Mastromonaco, Gunn, McCurdy-Adams, Edwards, & Schulte-Hostedde, 2014).

1.4.1.2. Infrared thermography - a potential measure of stress and animal welfare

In addition, infrared thermography (IRT), measured using thermal cameras (Figure 1.3), has been applied as a non-invasive measure of stress in animals (Jerem et al., 2018; McCafferty, Gallon, & Nord, 2015). It has been found that stress can cause the core body temperature to increase or decrease (Bouwknecht, Berend, & Paylor, 2007; Jerem et al., 2018; Ogata, Kikusui, Takeuchi, & Mori, 2006; Oka, Oka, & Hori, 2001) with a correlation between eye temperature and rectal temperature using the domestic cat as a model animal (Cook et al., 2001; Foster & Ijichi, 2017; S. R. Johnson, Rao, Hussey, Morley, & Traub-Dargatz, 2011; Ogata et al., 2006; Stryker, 2016). The thermal neutral zone for African lions in the Kalahari is suggested to be between 25° to 33°C (Smith & Kok, 2006). In Zimbabwe, the body temperatures using bio-loggers in lions under warm ambient conditions were between 37.4° to 39.1° C (Trethowan et al., 2017). Under basal conditions, a tiger's normal rectal temperature is 37.8°– 38.98°C (Nevill, Friend, & Toscano, 2004; Theobald, 1978). Body temperature can vary due to changes in the environment, reproductive status, ambient temperature, humidity, coat covering and shade. Varying their body temperature enables individuals to survive via metabolic or stress-induced effects (Jerem et al., 2018). This newer non-invasive

approach of using IRT needs to be validated further to confirm its reliability (Stryker, 2016).

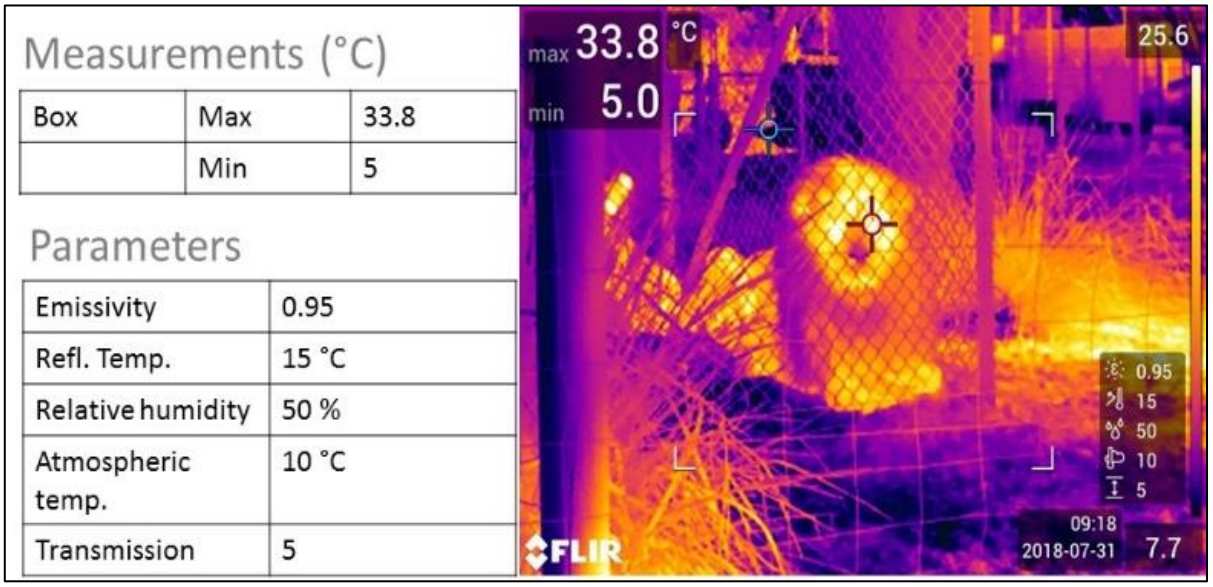

Figure 1. 3 Infrared thermography image of a captive male African lion (15 years old) to measure the eye temperature using infrared thermal camera FLIR during pilot study

1.4.2. Challenges of stress physiology research

Since most big cats are elusive and crepuscular in nature, collecting their biological samples is usually opportunistic and challenging. In the case of big cats living in groups, such as lions or others held together, identifying individual samples found in an area may be difficult. Also, collecting fresh samples may be inconvenient as the process may require intervention by the staff or management to acquire the fresh sample, especially if animals are on display in the exhibit areas. In the wild, this level of difficulty is further exacerbated as it is difficult to track uncollared wild big cats or to identify scat samples belonging to a particular individual.

1.5. Coping styles: Linking personality and stress for its implications to big cat welfare

A coping style consists of an external behavioural with an internal physiological stress response which is consistent over time and is characteristic to a certain group of individuals when faced with a stressor (Koolhaas et al., 1999). Animals may cope with stressors in their environment according to their personality. So even if different animals are exposed to same stressor, they may exhibit different coping styles (Broom, 1991; Carenzi & Verga, 2016). Individuals with a proactive coping style show more dominant and bold behaviours, being more aggressive towards conspecifics; individuals with a more reactive coping style show submissive behaviours and are less explorative (Carere, Drent, Privitera, Koolhaas, & Groothuis, 2005; Coppens, de Boer, & Koolhaas, 2010; Koolhaas, de Boer, Coppens, & Buwalda, 2010; Verbeek, Boon, & Drent, 1996).

The literature shows associations between personality types and GCs in animals, where certain traits may affect coping styles and levels of GCs or vice versa. An increase in GCs due to perceived stressor may lead to an animal reacting according to its personality that can affect the welfare of animals (Koolhaas & Van Reenen, 2016). This area is discussed very little for big cats (Vaz, McElligott, et al., 2022). For example, clouded leopards that were rated highly for fearfulness/tense, pacing, sleeping, self-injury and/or hiding behaviours, showed higher overall (base and peak) faecal GCs (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).

Certain personality types might benefit big cats by enabling them to adapt faster than others, while others may deal with stressors differently. Thus, understanding the personality types of big cats may provide useful cues in caring and making

management decisions for big cats. For example, fecundity in captive cheetahs was predicted by their 'tense-fearful' personality traits; understanding this contributed new insights towards solving conservation breeding problems (Wielebnowski, 1999). Providing these cats with good hiding spots could reduce the impact of stressors, as seen among cheetahs rated on tense-fearful scores or jungle cats with lower corticosterone levels (Marinath, Vaz, Kumar, Thiyagesan, & Baskaran, 2019; Wielebnowski, 1999).

Similarly, other behavioural traits have been linked to personality types and GC levels. Boldness may be linked to anxiety-related behaviours and to activity under stressful conditions (Gartner et al., 2014; Gartner & Weiss, 2013b; Rödel & Meyer, 2011; Torgerson-White & Bennett, 2014). Some empirical studies assume that boldness can also be expressed in exploratory behaviour (Carlstead, Brown, & Strawn, 1993). These findings suggest how much carers understand big cats' coping styles and personality can further affect the cats' level of welfare.

1.6. Human perception of welfare in big cats

Humans have many connections with animals such as pets, farm animals, backyard animals and/or others seen in nature reserves or zoos (Yerbury & Lukey, 2021). Yet, in considering the welfare of animals, different people emphasize different concerns– some, for example, explore basic health functioning and others examine the affective states. These concerns may differ according to the person's perceptions or interactions (Fraser, 2008). Human-animal interactions can be characterized as the degree of relatedness or distance between humans and animals (Estep & Hetts, 1992). It is affected by personal experiences, demography, societal experiences, cultural norms, expectations and beliefs, tolerance, and direct-indirect contact (Boogaard, Oosting, & Bock, 2006; Dickman, 2010). Te Velde *et al.* assert these perceptions may also be constructed according to a person's frames of reference, convictions or opinions, values, norms for translations of these values into code of conduct, knowledge

emerging from past experiences, facts or stories, and interests such as economic, social and moral (Te Velde, Aarts, & Van Woerkum, 2002). All these elements together may influence positive, negative or neutral perceptions towards animals.

The welfare of animals under regular human care receives most attention, with understandably lesser attention towards the welfare of animals in the wild. Of necessity, public perception research on wild animal welfare has been mainly captive or zoo animal centric (Davey, 2007b; Hassan, 2015; Melfi, McCormick, & Gibbs, 2004; Reade & Waran, 1996). Encroaching urbanization and loss of natural habitat however means there are increasingly more frequent interactions between humans and big cats. Any direct interactions with big cats can impact the lives of people and the animals (Treves & Karanth, 2003). This suggests more consideration in understanding public views on endangered species like big cats is required (Paquet & Darimont, 2010; Sainsbury, Bennett, & Kirkwood, 1995), especially to help change the perceptions of people who have had negative experiences. Building individuals' appreciation for wildlife and its nontangible benefits recognises that animal welfare and wildlife conservation are two sides of the same coin (Paquet & Darimont, 2010). It may also help to increase people's willingness to tolerate damage, successfully mitigate conflict and promote understanding (Conover, 2002).

In addition, public participation and stakeholder involvement can have the power to influence government decision-making and policies (R. E. Freeman, 1984; K. K. Miller & McGee, 2001). Both groups, depending on their levels of interest and influence in the subject, can be classified as "key players, "context setters," "subjects" and/or a "crowd" (De Lopez, 2001; Eden & Ackermann, 1998). In conservation projects, a stakeholder survey can provide community feedback on how they are being impacted. This information can inform initiatives that consider the needs of the people in the community and the needs of the animals (Grimble & Wellard, 1997). Heightened public awareness with increased understanding of human-wildlife conflicts can also

provide useful information into potential outcomes (Redpath et al., 2012). For example, interactions between various stakeholders can be useful to mitigate human-animal conflicts (Holland, Larson, & Powell, 2018). Such interactions may also help develop deeper community understandings of the multiple factors impacting human/ big cat interactions. At present, however, very little has been published in this area in the wider literature (Holland et al., 2018). However, the sentiments of stakeholders may hinder such collaborations if community members are against the issue. Especially in an urban landscape, which mostly favours development, stakeholders may be divided as pro-development or pro-environment, causing a dilemma regarding decisions for wildlife. Thus, there is a need to assess stakeholders' perceptions to more clearly understand diverse perspectives and develop ways to integrate their ideas.

1.6.1. Measuring human perception of big cat welfare

Human perception has been studied both quantitatively and qualitatively in the past. Quantitative data on human perception is concerned with measuring the magnitude or extent of a phenomenon, with predication and generalisation as the desired outcome of this technique. The qualitative research is concerned with describing humans' patterns of behaviour and processes of interactions, as well as revealing meanings, values and intentions of a person's life experiences. The data is then interpreted via various conceptual/theoretical perspectives (Creswell & Piano Clark, 2011). Both quantitative and qualitative methods have been used for assessing big cat welfare and each has benefits.

Quantitative methods consist of closed ended questions which can be collected through surveys or observations. Qualitative methods, in contrast, ask open ended questions, often in interviews or focus groups (Allen, 2017; Bryman, 2021). More recently, mixed methods have also been used. The term "mixed methods" refers to a methodology that integrates, or mixes, the quantitative and qualitative data within a

single investigation (Creswell & Piano Clark, 2011). Mixed methods can begin with a survey to find out the overall trends, followed by interviews to better understand the reasons behind these trends (Creswell & Piano Clark, 2011; Rossman & Wilson, 1985). Data collection may also be conducted the other way round depending on the research question. In the case of big cats and considering human interactions with the species may be limited to few stakeholders, understanding people's perceptions of these interactions is of crucial significance. Thus, stakeholder analysis is conducted across individuals associated with wild animals (Holland et al., 2018; Mushove & Vogel, 2005).

1.6.2. Challenges in incorporating human perception studies in big cat welfare

Identifying and assessing different stakeholders' perceptions can be a challenge as each stakeholder is unique. As Te Velde *et al.* observed, people's views about the welfare of animals are related to their frame of reference and goals. In many cases these may be economically or politically influenced, leading to positions for or against the cause (Verbeke, 2009). Thus, it is important to ensure the representation of all different groups to understand their role, and to garner the range of perspectives. Such multi-stakeholder involvement, while challenging to organise, has been applied to various areas such as the welfare of farm animals (Verbeke, 2009), mitigating conflict in various species (Redpath et al., 2004) and can provide mutual benefits and incentives to improve human-animal relationships. However, limited multi-stakeholder research has examined the issue of human interactions and perceptions on the welfare of big cats. This research helps address this gap.

There may also be challenges in collecting data. Sometimes while collecting data from various stakeholders, researchers may be treated as an outsider and the responses/participation may lack the depth of the issue. In addition, the interpretation of interviews can be biased, and inter-rater reliability needs to be validated.

1.7. Scope of the research

The overall aim of this thesis is to conduct research on matters pertaining to the welfare of big cats and make recommendations that could lead to better welfare (Figure 1.4). The research further aims to provide insights into the selection of appropriate methods to assist in the future success of reintroduction and conservation projects for big cats and promote their effective management. This thesis is a compilation of papers that are published and in progress. It is presented as a combination of the papers, with each paper/chapter addressing a specific objective.

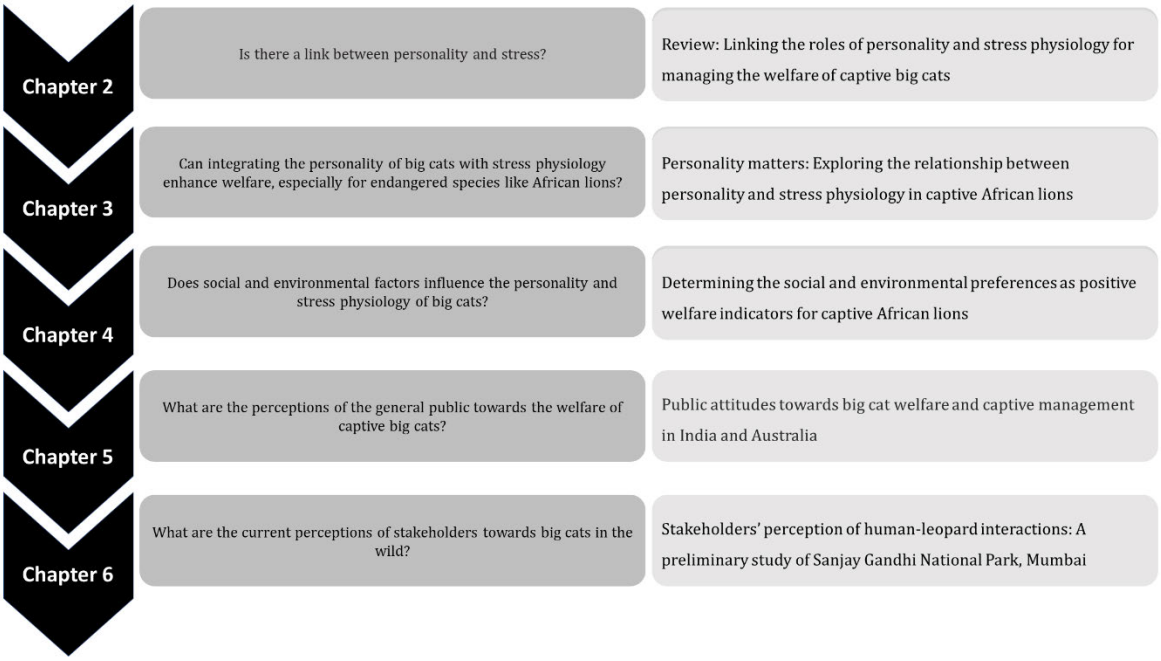

Figure 1. 4 The relationship between our main research questions

Building on this introductory chapter, Chapter 2 discusses the role of linking personality and stress physiology in big cats. The chapter identifies factors that may influence personality, GC levels and the integrated relationship of personality and GC in big cats.

Chapter 3 focuses on African lions and their personality types to examine if there is a relationship between personality and GCs. The chapter specifically investigates the influence of biological factors such as gender, age, and core body temperature, alongside the origin and location of the lion.

Chapter 4 assesses the social interactions, enclosure usage and enrichment preference of captive African lions using the association index, spread of participation index and electivity index. These indices are then compared with the lion's personality, cortisol levels, enclosure size and age to determine the driving factors affecting each lion's social and environmental preferences.

Chapter 5 assesses public attitudes towards big cat welfare and captive management in India and Australia.

Chapter 6 details human perceptions towards human-leopard interactions in the wild and assesses factors that may contribute to these perceptions.

Chapter 7 synthesises the results from the previous chapters and presents the final discussion. It then draws conclusions and makes recommendations for advancing and improving the welfare of big cats, both in captivity and in the wild, using modern tools and techniques to enhance the implementation of reintroduction programs.

Chapter 2: Linking the roles of personality and stress physiology for managing the welfare of captive big cats

Citation: Vaz, J, McElligott, AG, Narayan, E. (2022). Linking the roles of personality and stress physiology for managing the welfare of captive big cats. *Animal Welfare*. 31 (1): 99-111(13).

2.1. 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 role of GCs 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

2.2. 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 (Brambell, 1965; Harrison, 1964). 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 recognized as a key factor contributing to this variation (Finkemeier et al., 2018; G. J. Mason & Mendl, 1993).

Personality is defined as the set of behaviours exhibited consistently across time and situations (Finkemeier et al., 2018; Koolhaas et al., 1999; Réale & Dingemanse, 2012). 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. 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 hid more in a nest box compared to calm individuals (DeCaluwe, Wielebnowski, Howard, Pelican, & Ottinger, 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 (Finkemeier et al., 2018; Torgerson-White & Bennett, 2014).

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 a challenge or change that occurs in the

life of an animal that initiates a neuroendocrine stress response involving the release of hormones called catecholamines (rapid flight-fight response) and glucocorticoids (slow responding endocrine response) with acute or chronic effects (Schneiderman et al., 2005; Selye, 1973). While there is good evidence that acute stressors are associated with an increase in GC levels, these internal responses are generally thought of as healthy. There is also growing evidence that chronic stress, which may have negative consequences for an individual, are not always associated with increases in GCs (Boonstra, 2013). However, the way an animal perceives these stressors may also 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 GC 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, we still lack to understand what factors play a role in influencing the relationship between its personality and stress physiology. By identifying and understanding how the personality of big cats may predict stress responses, it is likely to promote more positive welfare outcomes for captive and rescued big cats. This review focusses on three essential topics to understand the underlying mechanisms of personality and GCs of big cats by: a) exploring the past literature on big cat personality and stress physiology for the overall scope; b) establishing the links between integrating these studies; and c) 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.

2.2.1. Historical and recent advances in big cat personality research

Most early personality research focused on understanding the different human personality traits and their application to daily life (Gartner, 2017; Gosling & Mehta, 2013). Later, studies of animal personality started being documented in numerous disciplines, but most of it was focused on non-human primate personality (H. D. Freeman & Gosling, 2010). It took a while for researchers to be 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 realization 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, Mendl, & Bateson, 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 (Baker & Pullen, 2013; Chadwick, 2014; Phillips & Peck, 2007; Torgerson-White & Bennett, 2014; Wielebnowski, 1999). 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).

2.2.2. Historical and recent 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 how it is perceived by an animal (Cockrem, 2013a; Morgan & Tromborg, 2007). 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, Olivier, & Koolhaas, 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). Exploring stress through glucocorticoids first began with invasive procedures where animals were culled to weigh their adrenals (Cannon, 1914). Later, this was done via surgically implanted infusion pumps for blood and plasma samples (J. L. 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 of them fell out of the normal mean range, yet they could indicate specific information for individual animals (T. D. Williams, 2008). This is now changing, as studies are including individual animal's stress response to improve individual welfare, thus advancing overall welfare.

2.3. 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 *Neofelis nebulosa*) and large sized cats of the subfamily Felinae (such as cheetah *Acinonyx jubatus*, 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.

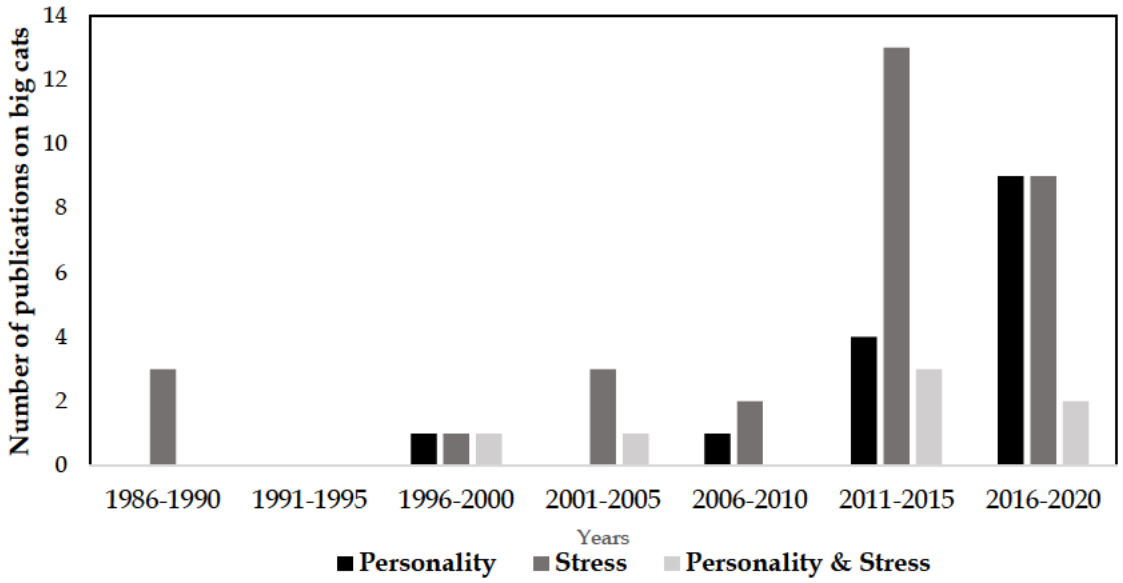

Figure 2. 1 Changing trends on published big cat personality and stress physiology research

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 physiology of big cats. These data were arranged chronologically by publication date to show changing trends over the years (Figure 2.1). 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 (Bertocchi et al., 2015; DeCaluwe et al.,

2013; Jurke, Czekala, Lindburg, & Millard, 1997; Torgerson-White & Bennett, 2014; Wielebnowski et al., 2002). 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 S2.1).

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

2.3.1.1. Personality

Over the years, studies on the personality of domestic cats have resulted in developing a comprehensive checklist of wild felid personality traits (Gartner et al., 2014; Phillips, Tribe, Lisle, Galloway, & Hansen, 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, Intraclass Correlation Coefficients (ICC) was 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 (R. A. 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, adventurous, 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, 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, Carere, Sgoifo, & Koolhaas, 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).

2.3.1.2. Stress physiology

The methods for assessing stress 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 hormones called glucocorticoids which are released in the form of cortisol and corticosterone (Oakley & Cidlowski, 2013; Sapolsky et al., 2000). 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 2.2).

GC 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.

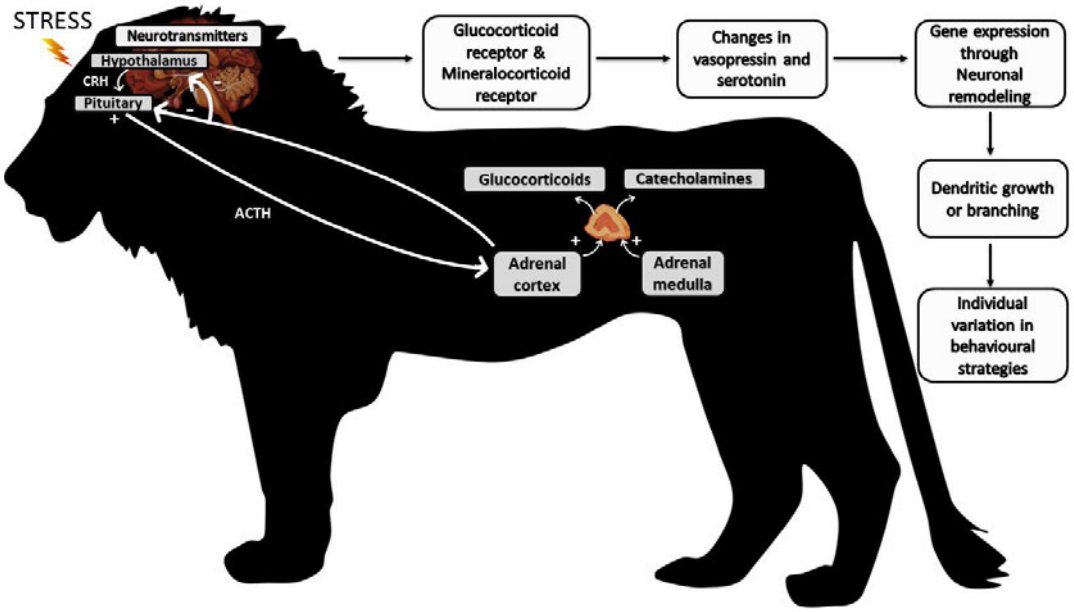

Figure 2. 2 The stress physiological pathway when a big cat is exposed to stressors; adapted from Caramaschi et al. (2013); (Matteri et al., 2000)

2.4. Linking personality traits and glucocorticoids 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 (Coppens et al., 2010; Koolhaas et al., 1999). 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 (Ellis, Jackson, & Boyce, 2006; Koolhaas et al., 1999). 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 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, Pisacane, & Miller, 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 GCs while indicating that there are some underlying factors that may influence this relationship.

2.4.1. Factors influencing the relationship between personality and glucocorticoids

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 2.3). Though these factors have been comprehensively studied across different taxa, there is limited information available for some factors on big cats. Exploring these gaps will provide a better understanding of the individual responses of big cats living in captive or rescued environments.

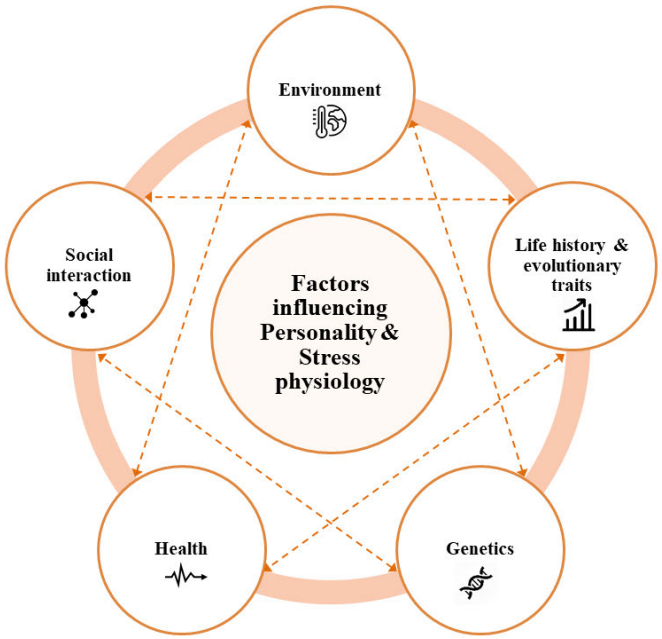

Figure 2. 3 Factors that play a role in the relationship between personality and stress physiology

2.4.1.1. Social interaction

The importance of social interaction and its role in shaping an animal's personality or GC levels is emphasized 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, Kaiser, & Hennessy, 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 maximized (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 species 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 (S. Kaiser, Hennessy, & Sachser, 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 GC levels. 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, Paini, 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 GCs of big cats.

2.4.1.2. 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 hideouts, 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.

2.4.1.3. 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 tightly 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 programs, 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 is necessary for survival in a wild population (Stamps, 2007; Wolf, van Doorn, Leimar, & Weissing, 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 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 changes to GCs 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 GC levels 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.

2.4.1.4. Genetics

Genes can influence both the personality traits and glucocorticoid levels of an individual (van Oers, de Jong, van Noordwijk, Kempenaers, & Drent, 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 have 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 explore gene-environment interactions (F. W. Allendorf, Hohenlohe, & Luikart, 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 (Carlstead & Shepherdson, 2000; Wielebnowski et al., 2002; Zayan, 1991). To date, little evidence has been found between the influence of genes on the personality and GCs of big cats. By 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.

2.4.1.5. 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 (Cavigelli, 2005; Friedman, 1990, 2008; 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 (Capitanio, 2011; Deary, Weiss, & Batty, 2010; Gartner, Powell, & Weiss, 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 the development as adults. Earlier research on the personalities of endangered big cats have been beneficial for estimating their health status and in future can contribute towards monitoring health and identifying illnesses in early stages (Gartner & Weiss, 2013b; Wang et al., 2019; Wielebnowski, 1999).

Big cats in captivity may have lower disease resistance with a weak immune system (Clubb & Mason, 2003; Morgan & Tromborg, 2007; Wielebnowski et al., 2002).

For example, a study examining the GCs of 20 captive cheetahs showed higher faecal corticoid levels than 20 free-ranging cheetahs, suggesting links to changes in metabolism, but the authors also speculate that high levels may be associated with chronic stress which could contribute to high morbidity, mortality and low reproduction rates among captive cheetahs (Terio, Marker, & Munson, 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, Antoniadis, & Morris, 2014).

Feline Immunodeficiency virus (FIV) weakens the immune system of big cats making them susceptible to infections (E. W. Brown, Olmsted, Martenson, & O'Brien, 1993). There are also instances of gastroenteritis in cheetahs and tigers associated with GC levels in captivity (Cociu, Wagner, Micu, & Mihaescu, 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).

2.5. Limitations and recommendations

Charismatic big cats often get 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 (Bertocchi et al., 2015; Touma, Sachser, Möstl, & Palme, 2003). 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 (Zoological Information Management System (ZIMS)). 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 is certainly

many opportunities for further research that could be carried out with reasonable sample sizes, especially if the research is multi-institutional in nature.

2.5.1. Limitations and recommendations from personality studies

Researching the personality of big cats has gained attention only recently. Keeper's attitudes can play an important role in promoting an animal's well-being. Literature on other species such as captive black rhinoceros, Chapman's zebra and Sulawesi crested black macaques shows unique keeper-animal dyads formed due to keeper's '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). When different keepers or researchers are asked to rate the same big cat, testing the inter-observer reliability of raters' will help avoid discrepancies among them.

2.5.2. Limitations and recommendations from stress physiology studies

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

Further, the commercial hormone kits are expensive and expire easily. Hence, over the years, researchers have been developing 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 standardization of these techniques could benefit

wild big cat conservation (Bhattacharjee et al., 2015; Mesa-Cruz, Brown, Waits, & Kelly, 2016; Pavlova, Ivanov, Kirluk, Rozhnov, & Naidenko, 2015).

2.6. Animal welfare implications and conclusions

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 summarizes 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 a part of conservation breeding programs, 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 programs. 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.

Acknowledgements

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

Conflicts of Interest

The authors declare no conflict of interest.

Chapter 3: Personality matters: Exploring the relationship between personality and stress physiology in captive African lions

Citation: Vaz, J., Bartley, A. & Hunt, J. (2022). Personality matters: exploring the relationship between personality and stress physiology in captive African lions. BMC Zoology 7, 30. https://doi.org/10.1186/s40850-022-00126-9

3.1. Abstract

Considering animals as individuals and not as species is becoming increasingly essential to animal welfare management in captive settings. Recent studies on big cat personalities and coping strategies suggest personality can help big cats cope in their surroundings. Yet a large portion of the published literature focuses on understanding either the personality or stress physiology of big cats. Our research shows how integrating an improved understanding of the personality of big cats with stress physiology may enhance welfare, especially for endangered species like African lions. By using a wild cat personality checklist, this study compared the key personality dimensions of 22 African lions with its faecal glucocorticoids and assessed factors influencing their personality and stress physiology. We found two reliable personality dimensions for African lions (dominance and agreeableness) and identified key factors (sex, age and location) that may influence their personality. Further, on testing if these factors influenced the stress physiology through variations in glucocorticoid levels, there was no significant difference. However, there was a strong negative association between agreeableness and glucocorticoid levels. These results suggest that the behavioural traits loading positively and higher for agreeableness are associated with lower glucocorticoid levels, which may assist a lion to cope with stressors in its surroundings. Our findings highlight this integrated approach of linking personality with glucocorticoids of big cats can be beneficial for caretakers. For example, during stressful veterinary procedures or in reintroduction programs, recognizing the personality of the lions can help in designing or providing them with resources that will alleviate stress. Thus, there is a need for more interdisciplinary approaches that will contribute towards enhancing the individual and overall welfare of big cats.

Keywords: animal personality, big cats, coping style, felids, stress glucocorticoids, welfare

3.2. Introduction

Improving the individual and overall welfare of big cats is an ongoing concern (Richter & Hintze, 2019). Previously, zoos around the world managed big cats following a standard set of husbandry protocols. These standards may include the guidelines for carnivores set by each zoological regulator, such as the husbandry guidelines for lions (Lion Care Manual, 2012). Australia manages captive lions under open range zoos, standard zoos, circuses, and rescue centres. In captivity, the welfare of these lions is a considerable concern, as it is difficult to mimic their wide-ranging natural habitat (Vaz et al., 2017). The 'one size fits all' welfare strategy does not recognise personality traits and may not be suitable to address individual animals' needs. Thus, more emphasis is being placed on understanding individual behavioural differences (Gosling, 2001; Wolfensohn et al., 2018). Individual differences, or animal personality, is defined as the set of behaviours exhibited consistently across time and situations (Finkemeier et al., 2018; Koolhaas et al., 1999; Réale & Dingemanse, 2012). One way of understanding a big cat's personality is by observing its behaviour or coping style in a challenging situation (Koolhaas et al., 1999; Vaz, McElligott, et al., 2022).

A coping style comprises an external behavioural with an internal physiological stress response; this response is consistent over time and is characteristic to a certain group of individuals when faced with a stressor (Koolhaas et al., 1999). Internally, the animal initiates a neuroendocrine stress response when faced with a stressor, that releases stress associated hormones called catecholamines (rapid flight-fight response) and glucocorticoids (slow responding endocrine response) with acute or chronic effects (Narayan et al., 2017; Schneiderman et al., 2005; Selye, 1973). However, the way an animal perceives these stressors may vary due to its personality, which is highlighted in its glucocorticoid (GC) levels (Caramaschi et al., 2013). Consistent individual variation in the stress physiology has been observed while measuring

cortisol in the hypothalamic-pituitary–adrenal (HPA) axis and assessing cardiovascular activity in the sympathetic–adrenal–medullary (SAM) system (Cockrem, 2013b; Soliemanifar, Soleymanifar, & Afrisham, 2018; Vaz, McElligott, et al., 2022). This individual variation is associated with GCs and has been linked to different coping styles, which are behavioural and physiological responses to a challenge (Koolhaas & Van Reenen, 2016). Certain personality traits may help individual felids cope better to perceived stressors. An example is the tendency among clouded leopards to hide: this tendency demonstrates fearfulness and correlates with higher GC levels (Wielebnowski et al., 2002).

A variety of behavioural tests and checklists have been developed in the past decade to help identify the personalities among big cats; these tests and checklists have been used for tigers (*Panthera tigris)* (Pastorino, Paini, et al., 2017; Phillips & Peck, 2007; Wang et al., 2019), jaguars (*Panthera onca)* (Boccacino et al., 2018), cheetahs (*Acinonyx jubatus)* (Baker & Pullen, 2013; Chadwick, 2014; Phillips et al., 2017; Wielebnowski, 1999), snow leopards (*Panthera uncia)* (Gartner & Powell, 2012; Gartner et al., 2016), and in particular the Asiatic lion (*Panthera leo persica)* (Goswami et al., 2020; Pastorino, Viau, et al., 2017) and African lion (*Panthera leo leo)* (Dunston, Abell, Doyle, Evershed, & Freire, 2016; Gartner et al., 2014; Kamyk, 2017). The multiple personality dimensions modified from human and primate studies on the Five-Factor Model (FFM) can be categorised as Openness to experience, Conscientiousness, Extraversion, Agreeableness and Neuroticism, abbreviated to OCEAN (Digman, 1990; Goldberg, 1990, 1992; McCrae & Costa, 1987). Previous studies on animals and wild felid personality have translated these human personality dimensions to suit feline behaviours to include dominance, which may not be very evident in humans (Gartner & Weiss, 2013a; King & Figueredo, 1997). Similarly, studies have examined the stress physiology of felids and variation in GCs through cortisol or corticosterone in blood, nail, saliva, urine, faeces and hair (S Creel, Christianson, & Schuette, 2013; Schildkraut, 2016; Sgambelluri, 2018).

Predominantly, a large portion of the published literature focuses on understanding either the personality or GCs of big cats. Of the seven studies that have focused on linking personality and stress in big cats, only one has studied this integrated relationship in African lions (Torgerson-White & Bennett, 2014). Their findings suggest that lions which were more social and less neurotic with unstable, nervous and negative affective traits, had lower GCs, indicating that more social animals coped better (Torgerson-White & Bennett, 2014). Previously, Gosling and John (Gosling & John, 1999) discussed that extraversion, neuroticism, and agreeable personality types were commonly seen across various species. However, many factors influence the relationship between personality and stress; these may be biological, social, environmental, life history and/or evolutionary traits, genetics and health (Gartner et al., 2014; Vaz, McElligott, et al., 2022). The influence of these dynamic factors may affect the animal, positively or negatively contributing to shaping its coping style. Investigating these factors specific to an individual lion may help to further understand the relationship between personality and variation in GCs.

This research explores the connections between big cats' personality and individuals' GCs to better understand individual animals' coping capacity and vulnerability to stressors (Koolhaas et al., 1999). The study specifically investigates the influence of factors such as sex, age, core body temperature through the eye, origin and location, on the personality and GCs of the African lions. Based on past research (Kamyk, 2017), we predict males would be more dominant than females, and have different roles according to their age. Also, due to separate biological functions between the sexes seen among cubs, sub-adults and adults, there is likely to be a difference in the GC levels between the male and female lions, although there is currently little consensus over the direction of this sexual dimorphism (Parnell et al., 2014; Wielebnowski et al., 2002). In addition, variation in the core eye temperature can be an indication of the perceived stressors, where higher eye temperatures are associated with higher GC levels and may also be linked with certain behavioural traits

as seen among dogs, cats and various big cats (Foster & Ijichi, 2017; Stryker, 2016; Travain et al., 2015). Similarly, the origin of the lion (zoo bred or a circus lion), along with its current location (zoo or a rescue centre without visitors), may influence its coping style. Further, it was expected that personality differences would correlate with differences in GC levels. Lastly, we investigated if any of these nominated factors may also impact the integrated relationship of personality and stress physiology.

3.3. Methods

3.3.1. Study sites and animals

Twenty-two African lions (13 males and 9 females) from two locations were studied between June-August 2018 and May-December 2019. There were eighteen lions (9 males, 9 females) at location 1 -Zambi Wildlife Retreat (ZWR) and four lions (4 males) location 2 - Sydney Zoo (SZ). Secondary demographic data about the lions such as sex, age and enclosure size were obtained from the study site records (Table S3.1). Zambi Wildlife Retreat is a retirement home for big cats from circuses, the entertainment industry or zoo breeding programs and is closed to visitors. Sydney Zoo is a newly opened zoo (2019), with lions relocated from another Australian zoo - Taronga Western Plains Zoo in Dubbo, NSW. Out of the 22 individuals, five geriatric lions had retired from a circus while others were raised in zoos. The age group of the lions was between 3 and 16 years (*Mean* = 9.1, *SD* = 4.9), and the lions were housed in enclosures that had an area ranging from 220 – 1500 sq.m. with conspecifics that were either male or females, except one solitary male whose sibling had passed away. To prevent unwanted breeding, all females were under a birth control program that involved the subcutaneous implantation of deslorelin acetate (Suprelorin® implant; Virbac).

3.3.2. Personality assessment for captive African lions

3.3.2.1. Data collection

Wild cat personality questionnaires and focal animal observations were used to create the personality profiles of the lions (Gartner, 2013; Highfill et al., 2010). The questionnaire, comprising 52 behavioural traits, was used to rate the lion's personality (Table S3.2). The traits were rated on a 7-point Likert scale, where 1 represents "not at all" and 7 represents "very much", describing the degree to which a behaviour is seen in an animal. For consistency in rating the animals, a definition list of each of these behavioural traits was shared with the keepers along with the personality checklist (Feaver et al., 1986; Gartner et al., 2014; Torgerson-White & Bennett, 2014; Wielebnowski, 1999). The lions were rated by five raters; four lion caretakers (two at each study site), and the researcher, who were all experienced in wild cat behaviour. The keeper ratings were based on their overall keeper interactions during daily animal care, veterinary procedures, and previous behavioural observations. These ratings were dependent on either experience with the animals or on existing knowledge of feline behaviours (Pastorino, Viau, et al., 2017). To reduce potential biases among keepers' ratings towards their favourite felid, the researcher observed lion behaviour following focal sampling methods on three random days from morning to evening and later completed the personality questionnaire (Altmann, 1974; Pastorino, Viau, et al., 2017).

3.3.2.2. Inter-rater reliability of behavioural traits

The Intra-class Correlation Coefficients (ICC) were used to measure the reliability of different raters. The mean ratings of the five raters (k raters) were run in RStudio version 1.2.5033 (RStudio, Inc. Boston, MA) to determine the ICC (3, k) scores (Koo & Li, 2016; Shrout & Fleiss, 1979). Behavioural traits with ICC values lower than 0.75 and confidence intervals overlapping zero were excluded from further analysis, as they

were deemed unreliable (Koo & Li, 2016). If a behavioural trait was excluded from one study site based on this definition, it was automatically excluded from the second study site to ensure that the same behavioural traits contributed to our definition of personality. Eighteen out of 52 behavioural traits passed Inter-rater Reliability testing across both study sites. The reliabilities of mean ratings ICC (3, k) ranged from 0.76 (trusting) to 0.99 (erratic) for lions at location 1 and 0.76 (clumsy) to 0.99 (vocal) for lions at location 2.

3.3.3. Faecal glucocorticoid assessment for captive African lions

3.3.3.1. Sample collection

Fresh faecal samples (< 2 days old) were identified and collected from individual lions during behavioural observations or cleaning routines, and a total of one to three faecal samples were collected per individual opportunistically (Table S3.1). These samples were collected only during the dry season as faecal samples remain stable for 5 days during the dry season, but for <1 day during the wet season (Mesa-Cruz, Brown, & Kelly, 2014). Each sample was labelled and stored temporarily at −20 °C at the zoo for 1-2 days, and later transported on ice to the laboratory and placed in the −80 °C freezer for longer storage until further analysis. Freezing samples without any chemical treatment at -80°C increases the recovery of glucocorticoids and was processed when all samples were collected (De Clercq, Vanden Bussche, Croubels, Delahaut, & Vanhaecke, 2014). It was ensured that samples were collected on random days by informing the keepers prior visitation to the zoo.

3.3.3.2. Hormone extraction and enzyme immunoassay (EIA)

The labelled frozen samples were then placed in a freeze-drier (Alpha 1-4 LD plus) for 48 hours to obtain a dried sample (Hunt & Wasser, 2003). The dried sample was ground using a mortar and pestle and sieved to attain a homogenised powder. 0.2 g of

this faecal powder was mixed with 2 mL of 90% ethanol and placed on an orbital shaker for 30 minutes. Samples were centrifuged for 15 minutes at 5000 rpm following the standard extraction protocol from Arbor Assays K003-H1W (DetectX®, Arbor Assays™). The supernatant obtained was stored, while the residue was discarded (Palme, Touma, Arias, Dominchin, & Lepschy, 2013). This supernatant solvent was then dried under nitrogen vapour (N_2) in a fume-cupboard - Dynaflow GRP. Later, using 400 µL of assay buffer, the dried sample extract was reconstituted with 100 µL of absolute ethanol and vortexed for 30 seconds.

The commercial DetectX® Cortisol Enzyme Immunoassay Kit K003-H1W (96 well plate) from Arbor Assays was used to analyse the levels of faecal cortisol. Following the manufacturer's instructions and previous studies on felids, the samples were processed (Narayan et al., 2013; Vaz et al., 2017). The plate map was used to map the layout of the samples, controls, and standards. The plate was read in a BIO-RAD iMark microplate reader at 450 nm. The final hormone concentration was calculated by multiplying the pg/mL hormone concentration with the final extract volume (0.5 mL) and dividing the faecal sample mass (0.2 g) to derive the final faecal cortisol concentration in ng/g of sample. An average of these values per lion was used for further analysis.

3.3.3.3. Assay validation for lion faecal samples

Since big cats such as African lions are classified as Vulnerable in the IUCN Red List Assessment (Bauer et al., 2016), acquiring permission to manipulate stressors in the study animals would not be permitted, especially for the retired lions due to welfare concerns. The Arbor Assays DetectX Cortisol EIA Kit has been tested and validated for various species such as Amur tiger, giraffe, kudu, Reeve's muntjac, white-handed gibbon, white rhino, zebra, and lion by the manufacturer in their product protocol (DetectX®, Arbor Assays™). We further confirmed this information from the manufacturing company via email (personal communication) and were provided with

a faecal glucocorticoid range. In addition, the Arbor Assays DetectX® Corticosterone EIA kit has been tested on African lions more recently (Fowler & Santymire, 2022). Therefore, we used the Arbor Assays EIA commercial kit that was already tested on the faecal samples of lions to assay the lions in our study. All faecal samples were assayed in duplicates and the sensitivity was reported as 27.6 pg/mL in the EIA Kit manual (product protocol, DetectX®, Arbor Assays™), while the limit of detection was 45.5 pg/mL. Further, our samples were within the linear range of the standard curve. These results indicate that EIA-K003-H5 kit is an analytically reliable assay for measuring cortisol concentrations in faeces of lions. The kit provides a mouse monoclonal antibody specific for cortisol to be detected in multi-species (DetectX®, Arbor Assays™). It also presents cross-reactivity with dexamethasone (18.8%), prednisolone (1-Dehydrocortisol) (7.8%), corticosterone (1.2%), cortisone (1.2%), progesterone (< 0.1%), estradiol (< 0.1%), cortisol 21-glucuronide (< 0.1%), 1 α - hydroxycorticosterone (< 0.1%) and testosterone (< 0.1%). We used three EIA plates to run the samples opportunistically. Average Intra-assay CV for Plate 1 (n=15) was 10.85%, Plate 2(n=28) was 5.31% and Plate 3(n=13) was 8.57% respectively. The average for Inter-assay correlation for two samples that were run between plates Plates 1 and 3 was 17.06% and Plates 2 and 3 was 9.34%. The repeatability between these duplicates were measured in RStudio version 1.2.5033 (RStudio, Inc. Boston, MA) using the ICC repeatability test (ICC = 0.77, 95% Class Intervals = 0.67, 0.87). Due to unforeseen circumstances while conducting the laboratory analysis, parallelism and recovery were not conducted during the experiment. We suggest that the results obtained here will be carefully used while addressing these limitations, and also suggest future studies to conduct a biological validation for every commercial EIA kit. A standard curve was plotted from synthetic CORT stock provided in the kit against its serial dilution. The samples were assayed in duplicates, with the mean of the two results being presented. To analyse if there was a significant relationship in the percentage of antibody bound between the standard

curve and serial dilutions, a linear regression analysis was used (Parnell et al., 2014)(R^2 = 0.9561) (Figure S3.1).

3.3.4. Investigating the factors influencing personality and stress physiology

Information on the sex, age, origin and location of the lions was obtained from zoo records (Table S3.1). To assess the core eye temperature, an infrared thermal (IRT) imaging camera -FLIR T530 was used. Thermographic core measurements were used to measure the temperature (◦C) in the lacrimal caruncle of each eye (Foster & Ijichi, 2017). Images of the focal lion were captured by standing at a distance of approximately 3-6 m to avoid any disturbance to the animals. The thermal images were uploaded in the FLIR Tools software to assess the core eye temperature by pointing to the hottest area around the eye (Jerem et al., 2018). The lions were observed every hour on observation days to ascertain each animal's average eye temperature.

3.3.5. Statistical analysis

3.3.5.1. Extracting the Principal Components and determining personality dimensions

For the 18 behavioural traits that passed the ICC reliability test, we used Principal Component Analysis (PCA) in IBM SPSS version 27.0 (SPSS Inc., Armonk, NY, USA) to determine the significant eigenvectors of personality. PCA reduces the dimensions by combining the original behavioural traits into a reduced number of orthogonal eigenvectors to represent the maximum variability of the covariance structure of the data (R. A. Johnson & Wichern, 2007). We considered eigenvectors as being significant if the associated eigenvalues were greater than 1 (Gartner et al., 2014; Litchfield et al., 2017) and eigenvectors were extracted based on the correlation (not covariance) matrix. The unrotated PCA indicated that 4 factors accounted for 80.53% of the variation in lion behaviour. However, we ran a parallel analysis that identifies factors having eigenvalues higher than values which may occur through chance that reduced

the significant eigenvectors extracted from the PCA to define our dimensions of personality in SPSS (Gartner et al., 2014; Horn, 1965; O'connor, 2000; A. M. Wood, Maltby, Stewart, & Joseph, 2008) (Table S3.3). The parallel analysis reduced the 4 components to 2 components explaining 62.99% variation (Table 3.1). Individual behaviours that had factors loading greater than 0.4 were viewed as biologically important behaviours that contribute to that eigenvector (Gartner et al., 2014). The feline personality dimensions were then determined either by assessing the continuum of one personality dimension such as bold-shy (Goswami et al., 2020) and by assessing multiple dimensions (Gartner et al., 2014; Litchfield et al., 2017). This study used the multiple dimensions of the FFM and included dominance for wild cats to ensure consistency in assessing big cat personality (Gartner & Weiss, 2013a; King & Figueredo, 1997).

3.3.5.2. Determining the effects of sex, age, core eye temperature, origin, and location on personality and stress physiology

We used a one-way analysis of variance (ANOVA) to examine the effects of sex, origin, and location on the PCA dimensions of African lions and the GC levels in SPSS. The level of significance, α, was set at 0.05. The PCA dimensions and cortisol levels were set as the dependent factor and sex, origin, and location as independent. In addition, linear regression was used to determine the relationship between PCA dimensions/cortisol and the age and core eye temperature of the lions.

3.3.5.3. Linking personality types with glucocorticoids and identifying factors influencing the integrated relationship

The resulting PCA personality scores were further used in investigating the relationship between PCA dimensions and cortisol levels using a Pearson's correlation. To identify the effects of the significant factors affecting this integrated relationship, a partial correlation was used, where the key factors were treated as

controlling variables when examining the relationship between personality and GC levels. Figures were constructed using the "ggplot2" package in RStudio version 1.2.5033 (RStudio, Inc. Boston, MA).

3.4. Results

3.4.1. Personality of African lions

3.4.1.1. Extracting personality axes

An examination of the total variance from unrotated Principal Component Analysis **(**PCA) indicated that four factors accounted for 80.53% of the variation in lion behaviour. However, parallel analysis indicated that only the eigenvalue of the first two principal components (PC) in the raw dataset exceeded these chance values, suggesting that these factors underlie the personality types (Table S3.3). Thus, the parallel analysis reduced the 4 components to 2 components explaining 62.99% variation and were labelled as PC1 and PC2, where a value of 0.4 or above was considered to be biologically important (Gartner et al., 2014) (Table 3.1).

Table 3. 1 Unrotated Principal Component Analysis of behavioural traits in African lions

While the original PCA revealed 4 PCs with eigenvalues greater than 1, parallel analysis reduced this to the first two PCs.

	PC1 Dominance	**PC2 Agreeableness**
Eigenvalue	6.831	4.508
% Variance	37.950	25.043
Loadings		
Active	0.245	**0.794**
Affectionate	**-0.702**	**0.457**
Bold	**0.500**	0.380
Bullying	**0.830**	0.123
Clumsy	0.238	**0.476**
Defiant	**0.653**	0.296
Distractible	0.225	**0.837**
Erratic	**0.902**	0.111
Friendly to people	**-0.666**	**0.539**
Gentle	**-0.922**	0.122
Inquisitive	-0.013	**0.810**
Inventive	**0.496**	**0.668**
Irritable	**0.858**	-0.123
Playful	0.074	**0.884**
Solitary	**0.484**	0.110
Stable	**-0.775**	0.299
Trusting	**-0.869**	0.382
Vocal	0.347	-0.170

PC1 explained 37.95% of the cumulative variance in the data representing a dominance axis. The traits erratic, bullying, defiant, irritable, bold, solitary and inventive loaded strongly and positively, while the traits gentle, trusting, stable, affectionate and friendly to people loaded negatively. Hence, lions having higher PC1 scores were bolder compared to those with lesser scores, indicating more dominant individuals.

PC2 explained 25.04% of the variance in the data representing an agreeableness axis. The traits of being playful, distractible, inquisitive, active, inventive, friendly to

people, clumsy and affectionate loaded strongly and positively. Hence, animals with higher PC2 scores were more agreeable, and those that scored low were more antagonistic. Based on the pattern of factor loadings, the two PCs were labelled as dominance, and agreeableness, respectively (John & Srivastava, 1999).

3.4.1.2. Effect of sex, origin, location, age and core eye temperature on personality

African lions rated higher for dominance differed significantly with sex; with males (*Mean* = 0.43, *SD* = 1.05) being significantly more dominant than females (*Mean* = -0.62, *SD* = 0.45) (Table 3.2). In contrast, male (*Mean* = 0.03, *SD* = 0.86) and female lions (*Mean* = -0.04, *SD* = 1.22) did not differ for agreeableness.

Table 3. 2 ANOVA results comparing the effects of sex, lion origin and lion location on personality

Personality type	Factors	SS	*df*	*F*	*P*
Dominance	Sex	6.008	1,20	8.016	**0.010**
	Origin	0.442	1,20	0.430	0.519
	Location	0.408	1,20	0.396	0.536
Agreeableness	Sex	0.036	1,20	0.034	0.856
	Origin	1.427	1,20	1.458	0.241
	Location	3.838	1,20	4.472	**0.047**

Origin of the lion did not differ significantly for dominance or agreeableness. Lions who were rated higher on agreeableness varied significantly between the location 1 – Zambi Wildlife Retreat (ZWR) (*Mean* = -0.19, *SD* = 0.91) and location 2 – Sydney Zoo (SZ) (*Mean* = 0.88, *SD* = 0.98), but not for dominance. Simple linear regression showed a negative relationship between dominance and age, with an R^2 of 0.136, but it was not significant (Table 3.3). However, there was a significant negative relationship between

agreeableness and age, with an R^2 of 0.342 indicating that agreeableness declines with age. Further, there was no significant relationship between core eye temperature and dominance or agreeableness.

Table 3. 3 Linear regression equation model to explore the relationship between age and core eye temperature on the intensity of personality types in captive African lions. The bold face values are significant at $P \leq 0.05$

Personality type	Factors	Std Coefficients		*T*	*df*	*F*	*P*
		Beta	**Std. Error**				
Dominance	Age	-.369	1.029	-1.777	1,20	3.157	0.091
	Core Eye Temperature	0.082	0.193	0.367	1,20	0.135	0.717
Agreeableness	Age	-.585	0.898	-3.222	1,20	10.381	**0.004**
	Core Eye Temperature	0.285	0.185	0.135	1,20	1.774	0.198

3.4.2. Stress glucocorticoid hormones

3.4.2.1. Cortisol levels of lions

The faecal GC concentrations ranged from 0.18 ng/g to 0.21 ng/g among the lions, with an overall mean of 0.20 ± 0.007 ng/g (Table 3.4).

Table 3. 4 Average cortisol levels (ng/g) for lions at both study sites

Lion	Average Cortisol (ng/g)
Males	0.202
Females	0.197
Study Site 1	0.201
Study Site 2	0.195

3.4.2.2. Effect of sex, origin, location, age and core eye temperature on stress physiology

Cortisol levels did not differ between sexes ($F_{(1, 20)}$ = 2.659, P = 0.119), with no individual difference between the males (*Mean* = 0.202, *SD* = 0.007) and females (*Mean* = 0.197, *SD* = 0.007). Similarly, there was no significant difference in cortisol with the origin of the lion ($F_{(1, 20)}$ = 1.128, P = 0.301), as the circus born African lions (*Mean* = 0.203, *SD* = 0.002) did not differ in their cortisol levels from zoo individuals (*Mean* = 0.199, *SD* = 0.008). In addition, there was no significant difference in cortisol among lions in the two locations ($F_{(1, 20)}$ = 2.092, P = 0.164), suggesting that the lions from SZ (*Mean* = 0.195, *SD* = 0.010) did not differ in their cortisol levels from ZWR (*Mean* = 0.201, *SD* = 0.007). Simple linear regression showed no relationship between cortisol and age (R^2 = 0.071, $F_{(1, 20)}$ = 1.529, P = 0.231) nor between cortisol and core eye temperature (R^2 = 0.001, $F_{(1, 20)}$ = 0.019, P = 0.892).

3.4.3. Relationship between personality types and glucocorticoids

There was a strong negative correlation (r = -0.533, P = 0.011) found between agreeableness and cortisol levels. In contrast, there was no significant relationship between dominance and cortisol levels (r = 0.196, P = 0.383) (Figure 3.1 and 3.2).

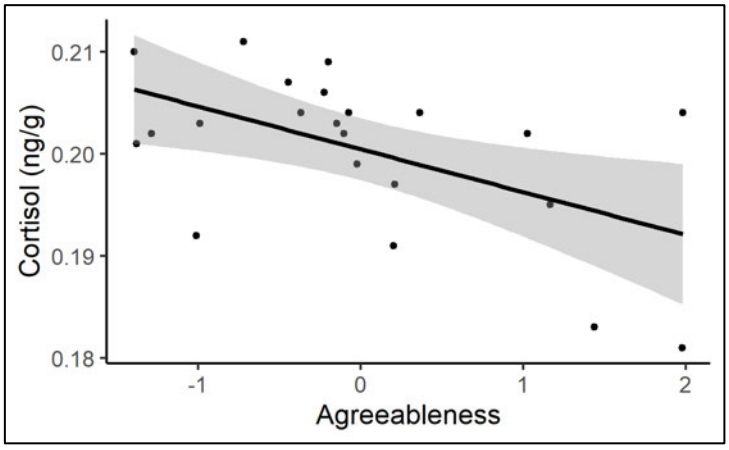

Figure 3. 1 Scatterplot showing the negative correlation between agreeableness and cortisol levels in African lions

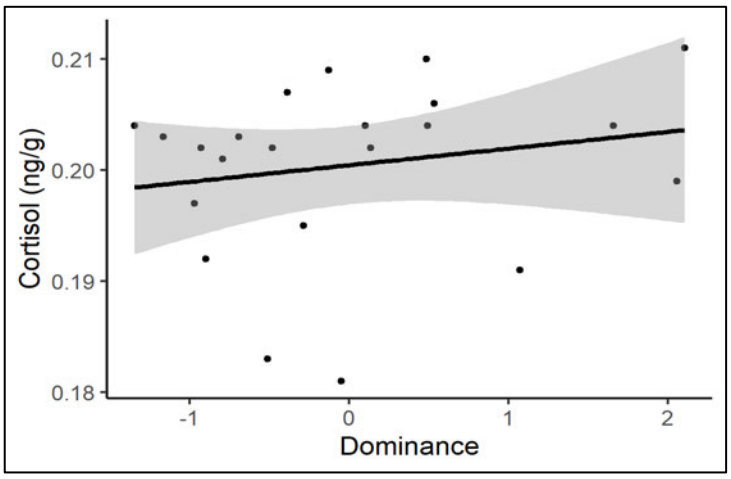

Figure 3. 2 Scatterplot showing the (non-significant) correlation between dominance and cortisol levels in African lions

3.4.3.1. Effect of key factors on integrated relationship of personality and glucocorticoid levels

A partial correlation was conducted on controlling the effects of sex, but there was no relationship (P = 0.946) found between dominance and cortisol levels. However, when controlling the effects of age and location, there was still a strong relationship between agreeableness and cortisol levels (P = 0.036).

3.5. Discussion

The present study assessed the links between the personality of African lions with their glucocorticoids to recognise factors that shape individual welfare. The personality of each lion was assessed by a rating method and the cortisol level was measured from fresh faecal samples (S Creel et al., 2013; Gartner et al., 2014). Further, our study quantifies the effects of factors such as sex, age, core eye temperature, origin and location on the personality of lions, followed by their stress physiology, and further on the integrated relationship of personality and stress. In short, we found two personality types among the studied African lions and found that sex, age and location of the lion may influence their personality. Further, on testing if these factors

influenced the stress physiology through GC levels, there was no significant influence. However, there was a strong negative association between agreeableness and GC levels.

3.5.1. Lion personality

The lions' behaviour at both study sites were reliably rated by the keepers and the researcher. From the reliably rated behavioural traits, two significant components comprising of the dimensions - dominance and agreeableness were found for African lions, which were similar to results reported for various wild cats (Gartner, 2015; Gartner et al., 2014; Torgerson-White & Bennett, 2014). Dominance loaded positively and strongly for behavioural traits - erratic, bullying, defiant, irritable, bold, solitary and inventive, while the behavioural traits gentle, trusting, stable, affectionate and friendly to people loaded negatively. Similarly, previous studies rated reintroduced African lions for their boldness, another term commonly used for dominance (Dunston et al., 2016) and Asiatic lions on a bold-shy axis for comparing individuals raised in captivity and others that were wild-rescued (Goswami et al., 2020). This suggests this dimension of dominance may be a prevalent trait among lions, and indicates that the social structure with roles of different individuals in a pride are important for their well-being (Gartner et al., 2016). For instance, from the behavioural trait loadings, the lions rated with high scores for dominance may want to compete and be the first to try everything, for example, in procuring food among others in a pride (Heinsohn & Packer, 1995), whereas lions rated with low scores for dominance are usually submissive and may avoid confrontation with other dominant individuals (Pastorino, Viau, et al., 2017). These findings were also comparable to studies where African lions rated lower for dominance were found to cope by hiding (Gartner et al., 2014; Heinsohn & Packer, 1995; Torgerson-White & Bennett, 2014).

The second dimension - agreeableness had the highest loadings for the behavioural traits playful, distractible, inquisitive, active, inventive, friendly to people,

clumsy and affectionate, loading strongly and positively. This dimension of agreeableness, though not discussed in the past for African lions, has been applied to other wild cats such as clouded leopards (Gartner et al., 2014) and domestic cats (Litchfield et al., 2017). Agreeableness may also be required for members of the pride to get along with each other to lead a social life. Lions with high scores for agreeableness are likely to represent cats that are coping well and potentially serve as a source of enrichment for other cats (Litchfield et al., 2017). In humans, exploring human personality has helped psychologists perceive the way people respond to stressors and have developed strategies to overcome them. Similarly, understanding the personality of lions can assist caretakers in ensuring their well-being by developing suitable approaches to cope with stressful circumstances such as veterinary procedures or reintroduction programs.

3.5.2. Lion glucocorticoid levels

In the literature, the levels of GCs may vary among individuals and these variations seem to be influenced by the time of day, health status, age, sex, personality, body condition, time of year, stage of breeding and the environment (Moberg, 1985; Vaz, McElligott, et al., 2022). Thus, even among lions managed in the same setting or among related individuals, there may be intraspecific metabolic variations in the GC levels (Carlstead & Shepherdson, 2000; Wasser et al., 2000; Wielebnowski et al., 2002; Zayan, 1991). In addition, other studies on African lions suggest that the variation found in GCs between individuals may act as markers to showcase the ongoing challenges faced by a lion (S Creel et al., 2013; Serres-Corral, Fernández-Bellon, Padilla-Solé, Carbajal, & López-Béjar, 2021). Thus, if the levels vary significantly and above the normal range of other individuals, it may reflect an imbalance (Schildkraut, 2016). Our results showed slight variations implying animal individuality, but it did not vary significantly between individuals. The literature suggests that studies have adopted different hormone extraction methods to measure faecal cortisol levels in lions (Vaz, McElligott, et al., 2022), where the average faecal cortisol ranged between 11.25- 22.00

ng/g (Serres-Corral et al., 2021) and 0.12-0.24 ug/g (Putman, Brown, Saffoe, Franklin, & Pukazhenthi, 2019). Our study contributes towards the existing knowledge of the cortisol levels in captive African lions. Despite the different settings of the two study sites such as public exposure, the mean cortisol levels did not vary significantly, which supports the literature that without additional challenges, the lions may not perceive stressors or be engaged in a coping style.

3.5.3. Factors influencing the personality dimensions and glucocorticoid levels of African lions

Our study assessed sex, age, core eye temperature, origin and location of the 22 lions to determine its influence on the personality types and stress physiology. On analysing the factors, we found that personality types were influenced by sex, age and location of the lion. Males were significantly more dominant than females. This describes the lions' social structure of living in a pride in a harem-style composition, as also discussed by Gartner et al. (2014). The lesser extent of dominance among females could support their egalitarian behaviour for their own survival and in communal cub-raising because their reproduction depends on synchronous breeding and overall group territoriality (Packer, Pusey, & Eberly, 2001). Previous studies have also suggested that male lions are more aggressive than females (S Creel et al., 2013), and it is also seen in other wild cats such as cheetahs where males scored significantly higher on the dominance and sociability dimensions than females (Baker & Pullen, 2013). Although previous studies found no significance of age on personality dimensions of African lions (Gartner et al., 2014) or cheetahs (Baker & Pullen, 2013), our results revealed that the younger individuals, more specifically lions aged between 3-7 years, were significantly more agreeable than older lions aged between 8-15 years. These variations may reflect the role of sub-adults and adults within pride behaviours (Dunston et al., 2016). For example, among reintroduced African lions, the sub-adults are more likely to be alert and active than adults (Dunston et al., 2016). In snow leopards, variance in curious/playful and active/vigilant was highest among mid-

aged animals and lowest in older animals, which are similar to our findings. Also, the variance in calm/self-assured was highest in the youngest snow leopards and lowest in older animals, which describes the traits for agreeableness seen among lions of different age groups (Gartner & Powell, 2012).

Secondly, lions at SZ (location 2) were rated higher for agreeableness than at ZWR (location 1). The small sample size at location 2 (n = 4) with younger aged individuals could result in these findings. Hence, a higher sample size or equal number of lions at both sites is essential to confirm this significance. Also, the limited sample size of having few rescued individuals from a circus versus those raised at a zoo, which varied across two locations (Table S3.1) could have resulted in such an outcome.

Contrary to the literature where males and females tend to vary in GC levels due to biological functions such as the differences in the amount of metabolites excreted, differences in plasma concentrations and differences in the structure (Touma & Palme, 2005), we did not find any difference in cortisol between the male and the female lions. However, past big cats' studies also do not have a consensus and sometimes have shown either males or females having higher GCs such as African lions (Schildkraut, 2016) Sumatran tigers (Parnell et al., 2014) and North American clouded leopards (Wielebnowski et al., 2002). It is possible that our results could be influenced by the contraceptive implants in the studied females that could suppress the release of GCs and decrease the adrenal steroid output (Putman et al., 2015).

In addition, the cortisol levels did not differ with the age across the two study periods. Similar findings were previously suggested for male African lions, where the concentrations of GCs were similar across age groups and did not vary with season (Putman et al., 2019). The cortisol levels also did not vary with the other factors – location, core eye temperature or origin, which is likely due to the unequal sample size as seen in personality results above.

3.5.4. Linking personality with glucocorticoids

Building an understanding of the connections between personality and GC levels in African lions may help enhance their management and well-being. In this study, between personality types and GC levels, there was a negative relationship between agreeableness and cortisol levels, with more agreeable lions having lower cortisol levels. This reveals that agreeable individuals may overcome challenges better than other individuals who are antagonistic. Lions rated on agreeableness were engaged in more playful behaviours and show other carefree traits such as distractible, inquisitive, active, inventive, friendly to people which may also help them to get along with other members of the pride. They may also perceive stressors differently and hence reflect lower cortisol levels as compared to other individuals in the pride, and which is seen among other species too (Antonevich et al., 2020; Boccia, Laudenslager , & Reite, 1995). These traits may help them to cope with a challenging situation. Although limited information is available on the integrated relationship of agreeableness and cortisol levels in human studies (Bibbey, Carroll, Roseboom, Phillips, & de Rooij, 2013; Oswald et al., 2006), there were similar findings suggesting that agreeableness may contribute to a reduced HPA-axis response in a real-life interpersonal conflict (Ode, Robinson, & Wilkowski, 2008).

Conversely, low scores for agreeableness may reflect poor socialisation and frustration (S Creel et al., 2013); these traits may be related to underlying health conditions as found among rescued domestic cats (Deary et al., 2010) and having higher cortisol levels (Burgener, Gusset, & Schmid, 2008). Previously, Ones *et al.* identified agreeableness correlates weakly with Extraversion, is negatively related to Neuroticism and somewhat positively correlated to Conscientiousness (Ones, Viswesvaran, & Reiss, 1996).

3.5.5. Avenues for future research

Although there are many benefits of linking personality and stress, there is very limited work published on big cats taking this approach. Our study contributes to establishing this relationship for captive African lions. Being aware of a lion's personality can help in caring for them more effectively and improving human-animal relationship. Maintaining a repository of the personality profiles of big cats' can be valuable for big cats' caretakers to enhance their knowledge of animals in their care and/or implement interventions such as veterinary assessments or enclosure developments. This information can also be useful for veterinarians to record health data.

We propose to record and store data on the personality and cortisol levels of big cats in the Zoological Information Management Software (ZIMS) that is accessible globally by ex-situ managers of zoos and rescue centres. Although it is expected that the reported GC concentrations would have resulted from different methodologies in sample collection, extraction and analysis, the storing of this data in a single online database will help to compare and contrast across the methods and further refine the technique beneficial for big cats. Only 1-3 faecal samples were collected for each individual lion which could be the reason for insufficient sampling to detect individual differences. For any labile trait, it is important to obtain multiple repeated measurements to get an accurate assessment of an individual's level of that trait (Wolak, Fairbairn, & Paulsen, 2012). The more variable the trait, the more samples needed to estimate repeatability. We also recommend conducting a biological validation before using every commercial kits, which may be conducted by using samples from a naturally occurring stressful event, such as the introduction of a new individual to the group, or a translocation from one enclosure to another. Due to unforeseen circumstances while conducting the laboratory analysis and the further impacts of COVID 19 and its limitations to rework with the samples, we hope this data can contribute to the existing literature.

Circulating hormones are metabolised extensively prior to excretion in faeces. GC metabolism is different for each species, and different GC assays bind to different GC metabolites. Therefore, it is critical to demonstrate that a specific assay is able to detect biologically relevant metabolites for a given species. For a pilot study like this, we used a biologically validated commercial cortisol kit on lions, after confirming from the company. The advantages of this study can then be applied to tailor animal welfare management specific to individual variation. For example, providing felids rated high on agreeableness with good hiding spots could reduce the impact of stressors, as seen among cheetahs rated on tense-fearful scores or among jungle cats with lower corticosterone levels (Marinath et al., 2019; Wielebnowski, 1999). In addition, a "less agreeable" cat with higher GC levels may need those hiding spots even more. Thus, this information is also beneficial in exhibit design, conservation reintroduction programs, species survival recovery plans to incorporate the needs while bringing a pride of social animals together.

3.6. Conclusions

In this study, two personality dimensions – dominance and agreeableness were identified for African lions. We found sex, location and age strongly related to two personality types, emphasising the social organisation of lions where males and females of different age groups play an important role in the pride. We also found that lions rated higher for agreeableness had lower cortisol levels, highlighting that their behavioural traits help them in developing better coping strategies. The current study further suggests developing and incorporating a more systematic approach in the management of individual lions in zoos, rescue centres or in reintroduction programs. The authors recommend that big cat management can collate personality and stress-related endocrine data into the Zoological Information Management Software (ZIMS), so it is accessible to big cat caretakers around the world. This would assist in

understanding the factors influencing personality and stress to help improve individual management and thus overall welfare for big cats.

Declarations

Ethics approval and consent to participate

All research procedures of this study (animal behaviour and faecal sample collection) were observational and non-invasive. We followed the 'Guidelines for the treatment of animals in behavioural research and teaching' (Buchanan et al., 2012) and the national laws on animal welfare for scientific research of Australia, where the research was conducted. Formal ethical approval for the research was granted by the Animal Care and Ethics Committee at Western Sydney University, New South Wales (A12772). Additionally, approval was given by the Biosafety and Radiation Safety Committee at Western Sydney University to work safely with the biological faecal samples (B12366). The participating rescue centre and zoo also granted permission to carry out research at their respective organisations and individual informed consent of the keepers was taken before administering the questionnaire about lion personality.

Consent for publication

Not applicable.

Availability of data and materials

The datasets used and analysed during the current study are available from the corresponding author on request.

Competing interests

The authors declare that they have no competing interests.

Funding

The study was supported by the Research Training Program Stipend from Western Sydney University to JV. JH was supported by a grant from the Australian Research Council (DP180101708). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Authors' contributions

JV and JH conceived and designed the study; JV and AB collected study materials, performed fieldwork and experimentation; JV and JH analysed the data and interpreted the results; JV wrote and prepared the manuscript; JV, AB and JH revised the manuscript. The authors read and approved the final manuscript.

Acknowledgements

The authors sincerely thank the staff of Zambi Wildlife Retreat – Donna Wilson, Tara Anderson, Brooke Burrows, and staff from Sydney Zoo – Sam Gilchrist, David French, Amanda Brady, Simon Husher for their support and assistance in data collection. We would also like to thank Dr. Edward Narayan, Dr. Alan G. McElligott and Dr. Stephanie Hing for their valuable suggestions in designing the study. The first author JV received training for the stress hormone analysis from Dr. Edward Narayan's Stress Lab.

Chapter 4: Determining the social and environmental preferences as positive welfare indicators for captive African lions

4.1. Abstract

Traditional animal welfare approaches are persistently evolving into a positive animal welfare (PAW) approach. While the former focuses on an animal's "needs", the latter focuses on an animal's "wants" which incorporates its emotional well-being. Understanding PAW with reliable positive welfare indicators can enhance the care of animals, especially for endangered species like big cats. In the case of African lions, living within a social pride in vast habitats, play a crucial role in their well-being. Consequently, the captive environment needs to explore and incorporate a lion's social and environmental preferences. It is proposed that assessing the lion's preferences using multiple indices can promote positive affective states. Thus, this study assessed the social interactions, enclosure usage and enrichment preference of 22 captive African lions using the association index, the spread of participation index and electivity index, respectively. These three indices were then compared with the lion's personality, cortisol levels, enclosure size and age, to determine the driving factors affecting social and environmental preferences. Our findings suggest that the lions' social interactions were negatively influenced by dominance personality types. Furthermore, lions rated higher on agreeableness showed some tendency to use secluded shaded areas with enrichment. These findings predict the social and environmental preferences of big cats and can facilitate designing enclosures with compatible prides during reintroduction programs.

Keywords: cortisol; enclosure usage; enrichment; felids; glucocorticoids; personality; positive animal welfare; social interaction

4.2. Introduction

Traditionally, animal welfare management was focused on satisfying the "basic needs" for captive animals by fulling the Five Freedoms, but this approach was limited, particularly when compared to peers in the wild (FAWC, 1979b; Fraser & Duncan, 1998). However, studies began recognizing that animals can experience feelings ranging from negative to positive, which further contributed to the development of the Five Domains Model (FDM) in 1994 (Boissy et al., 2007; Mellor, 2015). FDM comprises the following domains: nutrition, environment, health, behaviour, and mental state (Mellor & Reid, 1994). More recently, there has been an acceptance of animal sentience, comparing them to humans when they feel stressed or express emotions. This has encouraged moving forward from satisfying an animal's basic "needs" to an animal's "wants" or "preferences", which directly reflects the animal's desires to do so, leading towards positive animal welfare (PAW) (Dawkins, 1980; Lawrence et al., 2019). The wants and preferences of an animal can be defined as motivations to use the resources that an animal is surrounded by, among alternatives, and which stimulate its well-being (Kirkden & Pajor, 2006; Mellor, 2015). These PAW features are acknowledged alongside the Five Domains (Lawrence et al., 2019; Mellor & Reid, 1994) to allow an animal to choose conditions where they find comfort, contentment and other positive experiences while avoiding those which cause suffering or distress (Dawkins, 1980; Mellor & Beausoleil, 2015). Thus, PAW recognizes and considers an animal's emotional well-being and aims at promoting positive emotions, positive affective engagement, quality of life i.e., finding the right balance of positives over negatives and happiness i.e., how an animal feels most of the time (Lawrence et al., 2019; Webb, Veenhoven, Harfeld, & Jensen, 2019). There is increasing evidence to support the usefulness of PAW in pets and farm animals (Boissy & Erhard, 2014; Morton, 2007). With these known benefits, it is therefore essential to measure and validate PAW among all animals, with urgency in endangered species such as big cats.

In the wild, lions have vast territories and live socially in a pride. Due to the species-specific range of affiliative behaviours, lions have distinguished individualized relationships within a pride (Matoba, Kutsukake, & Hasegawa, 2013).

For example, lions can choose to spend time with certain members within their pride or may also show nomadic behaviours while moving around the habitat freely (Packer, Scheel, & Pusey, 1990). Furthermore, there is a growing consensus that individuals may spend more time with some members of their immediate pride while exploring habitats or using resources specific to their needs and wants (Heinsohn & Packer, 1995). In contrast, captive lions often share restricted spaces and limited resources with related or unrelated individuals, as the environment is controlled for them. These deprivations and ethical implications of captivity may be addressed through the practice of environmental enrichment that aims to enrich the lives of captive animals by identifying and providing stimuli with innovative modifications to the food, sensory, cognitive, social and physical habitat of the lions (Mellen & Shepherdson, 1997; Shepherdson, 1998). If the environmental conditions are suitable, lions may indicate their coping capacity by using the enclosure space homogeneously (Pastorino, Viau, et al., 2017; Ross, Schapiro, Hau, & Lukas, 2009; Troxell-Smith, Whelan, Magle, & Brown, 2017) with the enrichment items (Mellen & Shepherdson, 1997; Powell, 1995; Skibiel, Trevino, & Naugher, 2007), and ultimately by performing more species-typical naturalistic behaviours (Mellen & Shepherdson, 1997; B. G. Williams, Waran, Carruthers, & Young, 1996). Packer et al. (1990) and Chakrabarti and Jhala (2017) discuss that lions form partner preference groups within wild lion prides to forage and mate, and this might have adaptive benefits for compatibility, that are also important to the zoo settings. Therefore, understanding the social interactions, enclosure usage and enrichment preference of a lion can provide insights into its emotional state and "wants", which will promote PAW.

There has been more acceptance in the past few years to quantify the subjective states of the animals, which has improved the techniques used in measuring the welfare of emotional states of animals (Dawkins, 1980; Kirkden & Pajor, 2006). Previously various mathematical indices have been effective in assessing an animal's preferences, especially in social species such as wild dogs (*Lycaon pictus*) and elephants (*Loxodonta africana, Elephas maximus*) (Brady, McMahon, & Naulty, 2021; Brereton, 2020; de Villiers, Richardson, & van Jaarsveld, 2003; Fernandez & Harvey, 2021; Pinter-Wollman, Isbell, & Hart, 2009). Similar approaches of measuring the social

interactions, enclosure usage and enrichment preferences have been applied in felids using the association index (AI), the spread of participation index (SPI) and electivity index (EI) (Lyons, Young, & Deag, 1997; Pastorino, Brereton, Drago, Confalonieri, & Preziosi, 2021). The AI evaluates the closeness in the relationship among individuals within a group, and can further be represented graphically with sociograms; which is a social network diagram (Rees, 2015b). The SPI examines if the animal uses the enclosure space homogeneously (Plowman, 2003; Rees, 2015a). In the case of EI, the first experimental studies were used to measure the preference and utilisation of food types in relation to their abundance or availability in an environment (Vanderploeg & Scavia, 1979), but it has been applied to assess the utilisation of specific enrichment items depending on their availability in an enclosure (Lechowicz, 1982; Ross et al., 2009). Using such non-invasive techniques, these indices can overcome limitations presented by single-motivation choice tests, which involves rewards, deprivation or alterations in the surroundings (Kirkden & Pajor, 2006). Thus, our increased understanding of positive welfare indicators is based on assessing one or more of these social and environmental preferences in the African lion (*Panthera leo leo*) and Asiatic lion (*Panthera leo persica*) (Dunston et al., 2016; Lyons et al., 1997; Pastorino, Viau, et al., 2017).

Certain individual factors may affect a social animal's preference hence, we propose it may be influenced by its demography, personality, ability to perceive stressors and enclosure size (Vaz, Bartley, & Hunt, 2022; Vaz, McElligott, et al., 2022; E. Williams, Carter, Hall, & Bremner-Harrison, 2019b). In the wild, an animal's personality may influence their decisions in how they move or what risks they take while moving within a landscape (Kowalski, Grimm, Herde, Guenther, & Eccard, 2019). Similarly, in captivity, a lion's personality may influence its relationships with its conspecifics while using specific resources in an enclosure (Chadwick, 2014; Hedeen, 1982; Mosser & Packer, 2009; Sopelsa Hall, 2017). In addition, glucocorticoids such as cortisol may act as an indicator of an animal's response to various external events, further influencing its interactions with conspecifics or enrichment items (Koolhaas et al., 2001; Narayan et al., 2017). For example, dominant males may need to maintain their role while experiencing high levels of stress, or they may be faced

with short-lived daily effects of enrichment, feeding, management routines, veterinary procedures in captivity (Morgan & Tromborg, 2007). Through previous life experiences, animals may use preferred places or spend time with members to reduce fights or be in a state of distress, thus influencing their decisions in daily life. Lastly, as lions have vast habitats in the wild, enclosure size may affect their social and environmental preferences (Boissy et al., 2007; Mellor, 2015).

Thus, this study aims to investigate the social interactions, enclosure usage, and enrichment preferences of captive African lions by measuring the association index, the spread of participation index, and electivity index. Specifically, we tested if these preferences were driven by the personality, cortisol levels, enclosure size, and age of the African lions. Based on past research, we predict that the personality of a lion may influence its social interactions, as individuals with low sociable traits will have lower social interactions (Gartland, Firth, Laskowski, Jeanson, & Ioannou, 2021). Similarly, personality may affect space usage as more dominant lions will defend and use the enclosure space more homogeneously (Goswami et al., 2021; Goswami et al., 2020; Pastorino, Viau, et al., 2017). Also, personality may influence the enrichment preference, as more friendly individuals will be playful and explore enrichment items that would allow them to be curious (Powell, 1995; Powell & Svoke, 2008). In addition, stress responses may influence social interactions where higher cortisol levels may indicate submissive behaviour with lower social interactions (Blanchard, Sakai, McEwen, Weiss, & Blanchard, 1993) or vice versa where subordinates do not necessarily have higher GCs (Scott Creel, 2001). The cortisol levels may also influence or reflect the enclosure space usage of an animal, where individuals with higher cortisol levels may be submissive and restricted to using only certain spaces in the enclosure (Owen, Swaisgood, Czekala, & Lindburg, 2005). Likewise, individuals with higher cortisol levels and submissive behaviour may prefer using enrichment items that would help them hide from other conspecifics (Carlstead & Shepherdson, 2000). We predict that enclosure size may also influence social interactions; where larger enclosures may induce playful behaviours that would increase social interactions and allow animals to use the enclosure space homogeneously (Hogan, Houpt, & Sweeney, 1988; Ross, Calcutt, Schapiro, & Hau, 2011; Ross et al., 2009). Further, the enclosure

space may affect enrichment preference, with larger enclosures having more space for more diverse enrichment items and giving more choices to the animals (Newberry, 1995). Lastly, the age of the individual may influence its social interactions, where young individuals spend more time exhibiting playful behaviours and have higher social interactions (E. Williams et al., 2019b). Age may also influence the enclosure space usage, where younger individuals may tend to move around an enclosure more freely as compared to older cats that prefer resting more (Pitsko, 2003). Similarly, age may influence enrichment preference, with younger individuals showing a preference for play enrichment items (Videan, Fritz, Schwandt, Smith, & Howell, 2005). By assessing the lion's social and environmental preferences in relation to factors affecting it, this study aims to contribute and develop a holistic approach to studying the positive welfare indicators of African lions.

4.3. Materials and Methods

4.3.1. Study sites and animals

Data from twenty-two African lions housed at two locations – Zambi Wildlife Retreat (-33.86673807591927, 150.66920955389517) (n = 18) and Sydney Zoo (-33.789454048881666, 150.86756018087544) (n = 4) in New South Wales, were collected. Zambi Wildlife Retreat (ZWR) is a retirement home for big cats from circuses, the entertainment industry and zoo breeding programs; it is closed to visitors. Sydney Zoo (SZ) is a newly opened zoo (in 2019) with lions relocated from another Australian zoo - Western Plains Zoo, Dubbo, NSW. Out of the 22 lions, 13 were male and 9 were female. In addition, five of these individuals were circus-raised, while the other seventeen individuals were zoo bred. The age group of the lions was between 3 and 16 years (*Mean* = 9.1, *SD* = 4.9). The area of the enclosures ranged from 220 to 1500 sq.m., and some of these smaller enclosures were temporary homes for those individuals relocated from the circus. Since the study was conducted while some of these individuals were in their temporary enclosure, it was included in the analysis. The lions were housed with conspecifics that were either male or females, except one solitary male whose sibling had passed away. The enclosures comprised mainly of

natural soil substrates with several smaller grass areas and with enrichment items. The play enrichment items consisted of plastic cones or barrels and were placed randomly in the enclosure during the husbandry routine. These enrichment preferences of lions were included in the data collection, if the animal was seen playing with or using such enrichment items on the day of observation. The husbandry routine consists of cleaning the enclosure, randomly replacing sensory enrichment or play items and feeding the animals with meat five days a week at both study sites.

4.3.2. Social interactions

Social interactions among animals can be of various types, such as lying down, standing, walking side by side, playing, grooming together or sometimes showing negative interactions such as aggression (Cinková & Bičík, 2013; Rees, 1982). In this study, we measured all these associations as the number of times the two lions (dyads) were seen together in proximity, without the influence of other factors, such as food. Through scan sampling conducted every 30 minutes from 09:30 am - 3:00 pm, we recorded information about these dyads when the inter-individual distance was 2 meters or less (Caro, 1994; Chadwick, Rees, & Stevens-Wood, 2013). Due to the nature of the study being non-invasive, data were collected randomly on two days according to the convenience of the zoos. In addition, since we were collecting fresh faecal samples opportunistically linking to individual lions, we used the two days wherever possible that faecal samples were collected. However, in the case of where only a single sample was obtained from the lion, another random day of behaviour was observed.

Also, due to logistical constraints, the lions were observed during this time of the day, although they are considered crepuscular by nature in the wild. In addition, zoo individuals may be accustomed to activities occurring during the day at the zoo. Further, this study was conducted non-invasively without interrupting the regular husbandry routines, and care was taken to reduce the influence of our presence. During feeding time, some lions were isolated from the others in the holding area next to the enclosure, and those observations were excluded. Since Lion 15 was alone in the enclosure, it was excluded from the social network analysis. After collecting

information on dyads, the association index (AI) was used to determine the closeness in the relationship amongst lions in an enclosure (Pastorino, Viau, et al., 2017; Schaller, 1972). The association index was calculated as:

$$Association\ index\ (AI) = \frac{2N}{n_1 + n_2}$$

where

N = the number of times lions 1 and 2 were seen together (including when around other lions)

n_1 = the number of times lion 1 was seen (whether alone or with other lions)

n_2 = the number of times lion 2 was seen (whether alone or with other lions)

AI values range from 0 to 1, where 0 indicates that the animals were never seen together and 1 indicates that they were always seen together. After calculating AI, the relationship between dyads was graphically represented by creating sociograms (Rees, 2015b). Further, the AI for an individual lion was calculated by summing up the values of the dyad's association index that the individual belonged to.

4.3.3. Enclosure space utilisation

Data on the enclosure dimensions, design, and complexity of the eight lion enclosures were collected from zoo records and during field observations to the sites. A layout of each enclosure was obtained from Google Earth Pro and, depending on the size, shape and enrichment item, the enclosure was divided into unequal zones (Figure 4.1). Each zone was labelled, and the area of each zone was calculated using Google Earth Pro satellite images.

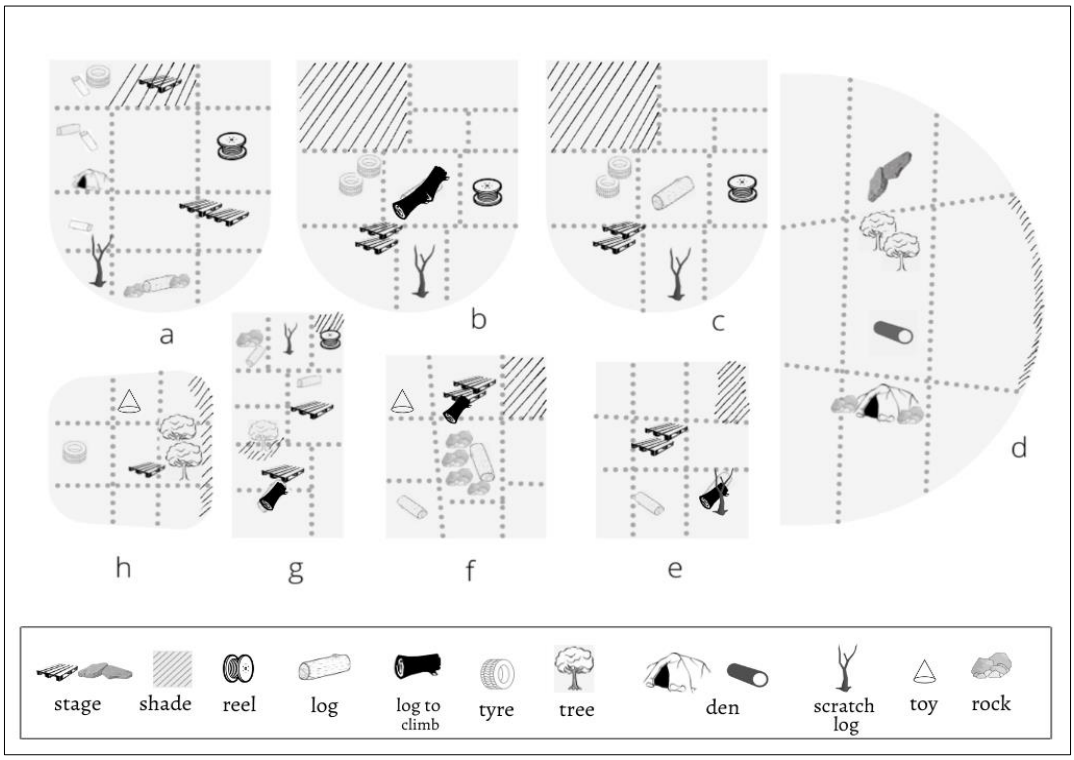

Figure 4. 1 Unequal zones of African lion enclosures a- h (n = 8) at two study sites in NSW

The enclosure usage of the lion was measured using the spread of participation index (SPI) as described by Plowman (Plowman, 2003) for unequal zones, which was modified from the equation by M. Dickens (1955) and Hedeen (1982). SPI for unequal zones was calculated as:

$$Spread\ of\ Participation\ Index\ (SPI) = \frac{\sum |f_o - f_e|}{2\ (N - f_{e\ min})},$$

where

f_o = the observed frequency of a lion in a zone

f_e = the expected frequency of a lion in a zone

$\sum |f_o - f_e|$ = the sum of the absolute value of the difference between f_o and f_e for all zones

$f_{e\ min}$ = the expected frequency of a lion in the smallest zone

N is the total number of observations of a lion in all zones

The observed frequency was measured by recording the location of the lion in a specific zone of the enclosure every 30 minutes from 09:30 am - 3:00 pm on two random days. The expected frequency was calculated by dividing the area of each zone to calculate the percentage of the area. SPI values can range from 0 to 1, where 0 suggests an even use of the enclosure while 1 represents the uneven use of the enclosure (Pastorino, Viau, et al., 2017; Plowman, 2003). The repeatability between SPI on Day 1 and Day 2 were measured in RStudio version 1.2.5033 (RStudio, Inc. Boston, MA). The SPI was repeatable for two days, the observation from both days was summed up and used for further analysis (ICC = 0.94, 95% Class Intervals = 0.88, 1.002) (Wolak et al., 2012).

4.3.4. Enrichment preference

Environmental enrichment was assessed in three steps. First, the enrichment items for each enclosure were categorised and counted (Table 4.1). These items consisted of both essential functional resources and non-essential resources which are aimed to reduce stress (such as places to recover from sources of handling or other stressors) and promote positive welfare (Marcon et al., 2018). Next, a scan sampling was conducted every 30 minutes for each lion from 09:30 am - 3:00 pm for two days, and the enrichment item being used by the lion was observed, irrespective of feed and non-feed days due to the study being opportunistic and non-invasive. Further, the preference for the enrichment item was assessed using the electivity index.

The electivity index (EI) of Vanderploeg and Scavia (1979) was calculated as:

$$Electivity\ Index\ (EI) = \frac{Wi - (1/n)}{Wi\ + (1/n)}$$

where

$$Wi = \frac{(\mathrm{ri/pi})}{\sum \mathrm{ri/pi}}$$

ri = observed use (proportion of time) of resource i and

pi = expected use (proportion of time) of resource i and

n = the number of types of resources

The observed use was assessed by observing the number of times an enrichment item was used by the lion during scan observations. Data from lions resting on the ground was excluded. The expected use was calculated by measuring the actual area of each of the enrichment items using Google Earth Pro and then dividing it by the total area of all the enrichment items together. The EI generated values between −1 and +1, where 0 to +1 indicates over-utilisation of a resource, and −1 to 0 indicates under-utilisation (Rees, 2015b).

Table 4. 1 List of enrichment items in the lion enclosures (*n* = 8) across both study sites

Enrichment item	Description of the enrichment area
Stage	slightly raised platform that is exposed
Shade	night cell or shaded area under cover
Reel	wooden cable reel
Log	log placed horizontally flat on the ground in the enclosure
Log to climb	log used for climbing onto heights
Tyre	rubber tyres placed around enclosure
Tree	introduced trees in the enclosure
Den	burrow or tunnel for animals to rest or hide inside
Scratch log	vertical log/pole with or without string attached
Toy	plastic barrel or ball or cone
Rock	introduced rocks (>0.5 m in length)

4.3.5. Individual variation in African lions– personality and cortisol levels

The personality and faecal samples for glucocorticoid analysis of African lions were collected between June-August 2018 and May-December 2019 and further analysed following the wild cat personality checklist (Gartner et al., 2014) and hormone extraction protocol (Narayan et al., 2013; Palme et al., 2013). A full description of the

steps used is described in Vaz, Bartley, et al. (2022), and a summary of this method is found below.

4.3.5.1. Personality

The wild cat personality checklist comprised 52 behavioural traits, that were measured on a 7-point Likert scale where 1 represents "not at all" and 7 represents "very much" for each lion (Gartner et al., 2014). Using the wild cat personality checklist, the lion's behaviour was rated by five raters, who were asked to undertake the questionnaire independently. Five different raters were used; four lion caretakers (two at each study site), and the researcher, but each lion was rated by only three people. These lion caretakers were working with their animals for at least six months, and to reduce the biases between the two keepers, the researcher completed the personality checklist after observing lion behaviour for two days. To test the reliability of different raters, the Intra-class Correlation Coefficients (ICC, (3, k) scores) were assessed in RStudio version 1.2.5033 (RStudio, Inc. Boston, MA) (Koo & Li, 2016; Shrout & Fleiss, 1979). The behavioural traits with ICC values less than 0.7 were excluded, which reduced them to 18 reliable traits (Koo & Li, 2016). The reliability of mean rating ICC (3, k) ranged from 0.76 (trusting) to 0.99 (erratic) for lions at Site 1 and 0.76 (clumsy) to 0.99 (vocal) for lions at Site 2 (Vaz, Bartley, et al., 2022). Further, these reliable behavioural traits were extracted using Principal Component Analysis (PCA) in IBM SPSS version 27.0 (SPSS Inc., Armonk, NY, USA).

4.3.5.2. Assessing cortisol levels

The cortisol levels of African lions were evaluated in three main steps – faecal sample collection, hormone extraction through enzyme immunoassay (EIA) and assay validation (Vaz, Bartley, et al., 2022). Fresh faecal samples were identified during behavioural observations by the researcher and collected by the caretakers during the cleaning routine. Since these samples were opportunistically collected, a total of one to three faecal samples were collected per individual and were stored at -20°C and -

80°C, and later freeze-dried before analysis. Following the standard extraction protocol from Arbor Assays K003-H1W (DetectX®, Arbor Assays™), samples were prepared for the enzyme immunoassay (EIA). The cortisol value (ng/g) for each faecal sample was then averaged to obtain the individual cortisol level per lion.

4.3.6. Age and enclosure size

The demographic details and enclosure size of the lions were obtained from zoo records.

4.3.7. Data analysis

Data were analysed using the software IBM SPSS version 27.0 (SPSS Inc., Armonk, NY, USA) and RStudio version 1.2.5033 (RStudio, Inc. Boston, MA). We first conducted the Pearson's correlation test between all the response variables – AI, SPI and EI to accurately estimate the relationship of the underlying variables (Table S4.5). Since there was no significant relationship among these three indices, we checked for a correlation between these response variables and the predictor variables - personality, cortisol levels, enclosure size, sex, and age (Carroll, 1961). A correlation analysis examines association, but it does not imply the existence of predictor and response variables. Sex was not included in the main model because there were no differences between males and females ($F(1, 20) = 1.605$, $P = 0.226$). Thus, all individuals were treated the same in further analysis. These data were analysed to test the influence of the predictor variables - personality, cortisol levels, age and enclosure size using standard multiple regression and to remove the effects of these predictors. The multiple regression explains the dynamics underlying a relationship by indicating which variables in combination may be more strongly associated with it. Thus, each predictor variable was regressed on the response variables AI, SPI and EI. Additionally, sociograms were created using the package "qgraph" in RStudio which categorised data into a matrix and later plotted with ggplot2 (Kolaczyk, 2014; Moreno & Jennings, 1938; Rees, 2015b).

4.4. Results

4.4.1. Indices exploring social and environmental preferences

Al scores per lion ranged from 0.250 to 0.917, revealing variation in the extent that lions interacted with their conspecifics. In addition, the sociograms illustrate individual relationships and the degree of association among the lions in an enclosure (Figure 4.2). The nodes represent individual lions (males or females) and the lines between nodes represent interactions between the lions in a group, while the thickness of the line represents the closeness of the relationship between individuals (Kamyk, 2017).

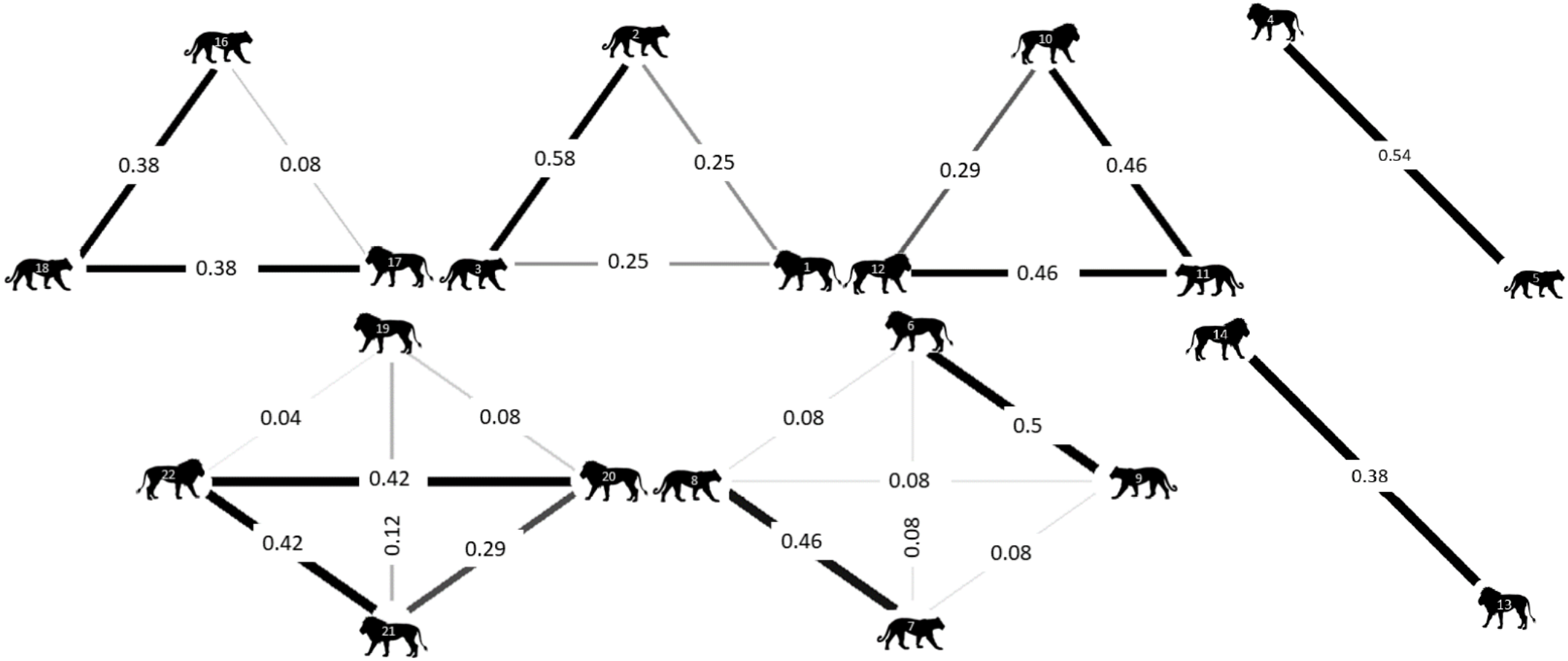

Figure 4. 2 Sociograms for lions observed at two study sites (represents male & represents female; darker lines indicate stronger bonds with more interactions)

The SPI values ranged from 0.442 to 0.909, which reveals that the lions used the space differently (Table S4.4). The possibility for Lion 19 to show a high SPI value with very uneven use of the enclosure could be because of a prolonged resting time following medication for a tooth injury.

A total of 528 scan observations recorded lions using an enrichment item or area. Lions preferred using different enrichment items in the enclosure, according to its availability. As shown in the table, some of these enrichment items were over-utilised while others were under-utilised (Table S4.3). Out of the enrichment items assessed, only two items such as the stage (exposed area) and shade area - were present in all the enclosures. Thus, the lions' preferences (EI) for stage and shade were used in subsequent statistical analysis with the AI and SPI (Table S4.4).

4.4.2. Individual variation (Personality and Cortisol levels of African lions)

Following the PCA, the behavioural traits were reduced to four components and based on the significant eigen vectors and parallel analysis, two components explained 62.99% variation (Table S4.1). Thus, the two key dimensions of lion personality were identified as dominance and agreeableness from the Five-Factor Model for wild animals, which were used for further analysis in this study (Goldberg, 1990; King & Figueredo, 1997).

The faecal GC concentrations ranged from 0.18 ng/g to 0.21 ng/g among the lions, with an overall mean of 0.20 ± 0.007 ng/g (Table S4.2). The EIA showed that the levels of cortisol varied between individuals, but not significantly.

4.4.3. Factors influencing social interactions, enclosure usage and enrichment preference

4.4.3.1. Effects of personality types, cortisol, enclosure size and age on the social interactions

Under the influence of all the predictor variables, the social interactions varied with personality. In the case of individuals rated higher for dominance, a negative relation

was seen between dominance and social interactions, suggesting that the more dominant lions showed lower social interactions among pride members (R^2 = 0.106) (Figure 4.3). However, age and other predictors didn't explain this relationship (Table 4.2).

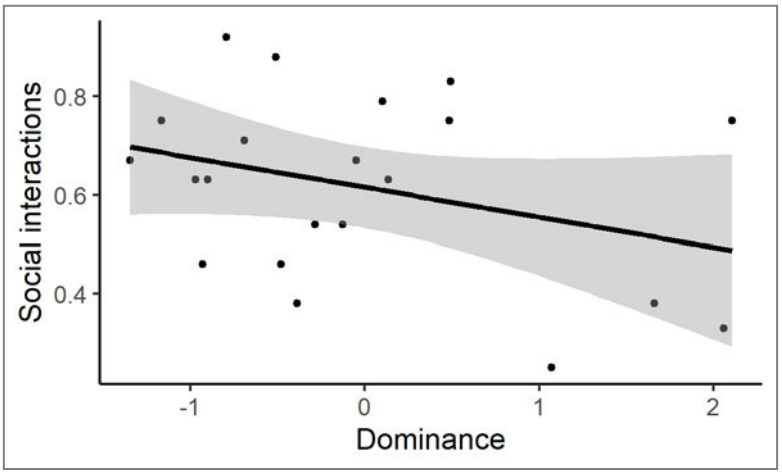

Figure 4. 3 The negative relationship between dominance and social interactions in African lions. This graph represents the relationship between the Principal Component scores for dominance and the social interactions calculated using the association index for 21 African lions. The trendline was produced using geom_smooth [ggplot2 package] of a linear model fit to the response variable AI (social interactions).

4.4.3.2. Effects of personality, cortisol, enclosure size and age on the enclosure usage of lions

Under the influence of all the predictor variables, the enclosure usage did not vary with personality, cortisol levels, enclosure size, and age (Table 4.2).

Table 4. 2 Multiple Regression examining the effects of personality types, cortisol levels, enclosure size and age on their social interactions, enclosure usage and enrichment preference. Estimates provided in boldface are statistically significant at $P < 0.05$.

Response variables	Predictor variables	Std Coefficients				
		Beta	**Std. Error**	***t***	***df***	***P***
Association index (AI)**	Dominance	-0.506	0.043	-2.180	*1,20*	**0.046**
	Agreeableness	0.07	0.058	0.219	*1,20*	0.829
	Cortisol	0.32	5.928	1.242	*1,20*	0.233
	Enclosure size	0.605	0.000	1.670	*1,20*	0.116
	Age	0.036	0.017	0.081	*1,20*	0.937
Spread of Participation Index (SPI)	Dominance	0.01	0.026	0.046	*1,21*	0.964
	Agreeableness	-0.045	0.034	-0.160	*1,21*	0.875
	Cortisol	-0.254	3.641	-1.034	*1,21*	0.316
	Enclosure size	0.01	0.000	0.034	*1,21*	0.973
	Age	-0.555	0.008	-1.569	*1,21*	0.136
Enrichment preference for stage (EI)	Dominance	-0.111	0.136	-0.537	*1,21*	0.599
	Agreeableness	-0.246	0.175	-0.924	*1,21*	0.369
	Cortisol	0.286	18.979	1.238	*1,21*	0.233
	Enclosure size	-0.133	0.000	-0.490	*1,21*	0.63
	Age	0.215	0.044	0.646	*1,21*	0.528
Enrichment preference for shade (EI)	Dominance	-0.075	0.122	-0.343	*1,21*	0.736
	Agreeableness	0.556	0.158	1.981	*1,21*	0.065
	Cortisol	0.131	17.088	0.541	*1,21*	0.596
	Enclosure size	0.406	0.000	1.424	*1,21*	0.174
	Age	0.083	0.040	0.236	*1,21*	0.816

** indicates analysis without Lion #15

4.4.3.3. Effects of personality, cortisol levels, enclosure size and age on the enrichment preference (stage or shade) of lions

Under the influence of all the predictor variables, the preference for stage or shade did not vary with personality, cortisol, enclosure size and age (Table 4.2). In the case of agreeableness, there was a slight positive relation seen suggesting that lions rated higher for agreeableness preferred using shaded enrichment area ($R^2 = 0.330$), but it was not significant under the influence of other variables.

4.5. Discussion

The present study assessed the social interactions, enclosure usage and enrichment preference of African lions using indices such as AI, SPI and EI, respectively. Our findings suggest lions differ in their social interactions, enclosure space usage, and in their preferences for enrichment items. We assessed the influence of various factors such as personality, cortisol levels, enclosure size and age, and found that the social interactions were negatively related to dominance personality type. Furthermore, there was a slight positive relationship between agreeableness and the preference for shaded areas with enrichment items. Here, we discuss these factors in detail.

In the past, the dynamics of social interactions have been predicted by an animal's personality for various species, such as gorillas, elephants and there is increasing evidence of its relevance for wild felids (Dunston et al., 2016; Racevska & Hill, 2017; E. Williams, Carter, Hall, & Bremner-Harrison, 2019a). From the two personality dimensions (dominance and agreeableness) identified in this study, lions that were rated higher for dominance displayed lower social interactions. This may relate to the social structure of African lions which consists of 'fission-fusion' social units, either comprising a male with four-six related females with or without offspring or sometimes as a coalition of unrelated males, while some others show nomadic behaviours (Schaller, 1972; Sogbohossou et al., 2014). Due to competition for resources in the wild or an enclosure, dominant individuals are highly territorial and control resource allocation among conspecifics through dominant and territorial behaviours (Mosser & Packer, 2009; Packer et al., 1990; Sundstrom & Altman, 1974). The traits defining this dimension - erratic, bullying, defiant, irritable, bold, solitary and inventive loaded positively, while the traits gentle, trusting, stable, affectionate and friendly to people loaded negatively among the studied lions, which explains behavioural traits leading to lesser social interactions. These dominant individuals tend to spend more time solitary without interacting with others, as compared to individuals rated for agreeableness. This trend also indicates that in a socially cohesive pride, socially influential keystone individuals have specific roles for maintaining social connection (Abell et al., 2013).

Space usage is of great importance for felids to display their natural behaviours, but only a few studies have measured the effect of personality on their environmental preferences (Baker & Pullen, 2013; Pastorino, Viau, et al., 2017). Contrary to the findings of a study conducted on Asiatic lions, where the enclosure space usage varied according to the personality types (Goswami et al., 2020), the enclosure space usage of African lions in our study did not vary according to their personality types. The resources available in the enclosure may stimulate the physical and behavioural needs of an individual, and the expected activity budget for any species is likely to have a significant impact on enclosure usage. A species such as African lions is anticipated to spend large proportions of its day resting and sleeping (Schaller, 1972), so the areas within the enclosures that promote these behaviours would be expected to be used for a higher proportion of the time. Similarly, areas that promote active behaviours could be expected to be utilised less in this species during the day that are adapted to only be active for a small proportion of its activity budget. This may not be indicative of poor welfare but a natural behaviour pattern. However, we would need more research in this area to explore if space usage is linked to a lion's personality.

Furthermore, providing felids with enrichment items allows them to express their natural behaviours (Mellen & Shepherdson, 1997), and assessing the EI may indicate whether an individual has a preference amongst alternative resources in an enclosure. Each enrichment item available and assessed for the animals in this study may promote a different behaviour and the natural duration of that behaviour may further vary, for example, the expected time spent on resting in shade vs expected time scratching a log may vary tremendously. Our results demonstrate that lions showed a slight preference for the use of enrichment items in the enclosure, with similar findings reported for Asiatic lions (Goswami et al., 2021). While there was no preference for the stage usage, it was observed that there was a slight preference for the shade usage, especially for lions rated for agreeableness. These lions over-utilised the shaded areas more than the others. The shaded areas promote more privacy, and it appeared to be well-suited for agreeable animals who could find comfort and feel less stressed to then go back to showing their natural behaviours (Marinath et al., 2019). However, the preference of resources such as shaded areas may be utilised

differently during periods of hot or cool weather conditions and need to be carefully understood in future. Overall, personality may be considered a predictor of social and environmental preferences for addressing individual lion welfare.

Social stressors are often discussed in the literature, mostly indicating that subordinate animals have higher plasma catecholamine and corticosterone, (Vaz, McElligott, et al., 2022; Zayan, 1991) and variations in cortisol among dominant individuals in captivity could be a result of external events such as veterinary procedures or feed days (Kleiman, 2010; Morgan & Tromborg, 2007). Our results show no significant relationship between the cortisol levels and social interactions of the lions, which could indicate that these individuals were habituated to living with their conspecifics. Being in a familiar group may provide a lion with strong social support and such individuals are usually less adversely affected by stressful situations (Dantzer, 1990).

Assessing the glucocorticoids via cortisol can also reveal the internal coping mechanism in relation to the external choices made by an animal for the enclosure (Koolhaas et al., 2001; Vaz et al., 2017). This study found no significant difference in the enclosure usage under the influence of the nominated factors, which may indicate that the lions feel less anxious due to increased familiarity within a limited home range or enclosure, as also seen in other species of mammals and birds (Dawkins, 1977; DeRango et al., 2019). Past research assessing enrichment intervention effects found that faecal corticosterone levels in a test group of Asiatic lions lowered from the baseline, while it remained unchanged for the control group, revealing a vital inter-linkage between physiological and behavioural indices of welfare (Goswami et al., 2021). However, the use of enrichment may also vary due to dynamic external conditions, such as ambient temperatures. For example, pigs would rest on straw in the morning when it is cold, but not in the evening when it is warm (Fraser, 1985; Steiger, Tschanz, Jakob, & Scholl, 1979). Thus, performing preference tests with measures of deprivation, frustration and distress may also determine the enrichment items preferred for an individual's welfare (Kirkden & Pajor, 2006). Nevertheless, our study was non-invasive and since we did not perform any enrichment intervention,

the animals were habituated to using the enrichment items and there was no significant difference in enrichment preference with the varying levels of cortisol.

Being in an environment that suits an animal's needs may positively affect social interactions (Boissy et al., 2007). As captive animals may not perform all natural behaviours as their peers in the wild, such as foraging, travelling or territorial defence; they may dedicate more time to social interactions (Matoba et al., 2013). However, we did not find a relationship between enclosure size and social interactions. Some of the enclosure sizes were small and below the recommended measurements for lions in captivity according to the Exhibited Animals Protection Act 1986 standards and the NSW Department of Primary Industries report, which could prohibit the natural behaviours (The NSW Department of Industry Skills and Regional Development, 2016). Among newly introduced animals, the larger enclosures may provide space to hide or reduce aggression, but among familiar individuals, social interactions may be determined by prior experience and not enclosure size (Valuska & Mench, 2013).

With modern zoos providing larger enclosures for big cats, we assessed if enclosure space usage could be predicted by enclosure size. Our results reveal that the enclosure usage did not vary according to the enclosure size, which could indicate that the size of the enclosure alone does not matter, but it may be influenced by various factors. This is similar to the findings where big cats in bigger enclosures had a higher level of apparent movement, but only about fifty percent of enclosure space was used (Lyons et al., 1997). This shows that more than the amount of space available, it is the quality of the space made available that matters, which may be associated with the enrichment items (Woods, Lane, & Miller, 2020). However, we found no significant difference between enrichment preference for stage or shade according to the enclosure size. It may be predicted that having only one enrichment item in quantity may restrict all lions from having access to it and be unavailable to the others, unlike in the wild context where animals are free to choose from a range of similar items. Thus, the standard recommendation of having one stage or shade area in an enclosure due to space constraints may hinder the positive welfare of lions by restricting access to resources according to their preferences. The EI scores may also highlight that lions may avoid enclosure zones that are regularly used by other individuals, as seen

between two female leopards (Pastorino et al., 2021). Thus, EI may also reflect an animal using an enrichment item due to the unavailability of desired items or to either avoid or spend time with some individuals and not only as a preference.

Age-specific behaviour can influence grouping patterns among lions. The social interactions between age classes may facilitate recruitment or dispersal of individuals where sub-adult male lions in the wild may disperse from their natal pride and form coalitions with other dispersing subadult males (Mbizah et al., 2020; Orsdol, Hanby, & Bygott, 1985). In addition, the presence of cubs in a pride can lead to lesser interactions among females, which becomes balanced as the offspring matured (Kirk & Wascher, 2018). As our study consisted of sub-adults and adults-only, there were more balanced social interactions without much variation between the groups, as described in the literature. Similarly, age did not influence enclosure space usage, nor for the use of enrichment items. As younger cubs would spend more time in play behaviour, it would be likely for them to use certain areas in the enclosure or the enrichment items (Clubb & Mason, 2007; Ncube & Ndagurwa, 2010). However, among sub-adults and older individuals, other than age, other factors may influence their enclosure space usage and enrichment preference (Macdonald & Loveridge, 2010).

By understanding the social interactions of a lion with its personality, there is scope to identify its preferences and further contribute towards its positive well-being (Dawkins, 1990, 1998). Thus, the grouping of individuals after recognizing their personality may help in reducing aggression, alleviating stress, and promoting more naturalistic behaviours. Since dominance reduces social interactions, providing these individuals with larger areas may help them avoid being close to other individuals constantly. We encourage caretakers to incorporate the assessment of social interactions, which will inform them about the social well-being of their lions and help promote positive outcomes for big cats. However, assessing the social interactions with the AI gives values for dyads, but not for individuals. We overcame this limitation by summing up the AI values involving the same individual and recommend using this method. Although some lions in this study were circus-raised individuals and may pose a limitation when compared to lions in other captive

settings, we believe that this study has the merits to showcase positive welfare indicators by focusing on individual welfare.

Positive welfare can further be improved by understanding the preferences and how an animal feels in its environment. The findings of this study suggest the importance of providing lions rated higher on agreeableness with continuous access to a shaded area with some privacy that may suit their needs. Knowledge about a lion's preferences can be extremely useful in reintroduction programs, where animals may be selected and kept in a pre-release facility to encourage bonding with unfamiliar individuals to form cohesive groups in unfamiliar surroundings. In addition, assessing the unique personality traits within the group and providing various enrichment interventions specific to these individual differences can be useful to the big cats' welfare. More recently, the University of Birmingham in partnership with local zoos designed an interactive interface - The Enclosure Design Tool for apes and parrots to compare the behaviour of captive or rescued individuals to those of their wild peers, which will be beneficial to apply across other species in future (University of Birmingham). By using such tools, there is scope to design complex enclosures with a natural social structure to suit individual animal's preferences. For example, assessing a lion's personality can provide insights for establishing compatible groups and further introduce enrichment items that would promote their welfare, such as hiding spots or exposed heights. We also suggest that upcoming studies could focus on having a strong demographic representation of prides with comparable size and age groups to expand this study.

4.6. Conclusions

The three indices reported in this study (association index, spread of participation index and electivity index) extend our understanding of the social and environmental preferences of captive African lions, and the factors that may shape these preferences. We found that the social interactions of African lions were negatively influenced by dominance personality types, while agreeable lions preferred using secluded shaded areas. These results are useful for assessing how animals share resources, interact with

each other within their enclosures and may prevent exclusion of certain members. Thus, determining the social and environmental preferences may be applicable to house lions in future ex-situ programs and could possibly be extrapolated to other social species.

Ethics statement

Formal ethical approval for the research project was granted by the Animal Care and Ethics Committee at Western Sydney University, New South Wales (A12772). Additionally, approval was given by the Biosafety and Radiation Safety Committee at Western Sydney University to work safely with the biological faecal samples for stress associated hormone analysis (B12366). The participating rescue centre and zoo also granted permission to conduct the study and informed consent was obtained from all subjects involved in the study.

Funding

The study was supported by the Research Training Program Stipend from Western Sydney University to JV. JH was supported by a grant from the Australian Research Council (DP180101708). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Authors' contributions

JV and JH conceived and designed the study; JV and AB collected study materials, performed fieldwork and experimentation; JV and JH analysed the data and interpreted the results; JV wrote and prepared the manuscript; JV, AB and JH revised the manuscript. The authors read and approved the final manuscript.

Acknowledgements

The authors sincerely thank the staff of Zambi Wildlife Retreat – Donna Wilson, Tara Anderson, Brooke Burrows, and staff from Sydney Zoo – Sam Gilchrist, David French, Amanda Brady, Simon Husher for their support and assistance in data collection. We would also like to thank Dr Edward Narayan for training the first author JV in stress hormone analysis. The authors also thank Orvill Nazareth and Dr Russell Thompson

for their valuable suggestions for data visualization and Dr Susan Mowbray on the initial write-up.

Chapter 5: Public attitudes towards the welfare of captive big cats in Indian and Australian zoos

5.1. Abstract

Human attitudes can play a key role in influencing the welfare of animals. Individuals with positive attitudes towards preferred species are likely to show more care and concern towards their welfare. These attitudes may further vary with demography, social factors and understandings of animal welfare. Although tremendous interest is often shown towards the charismatic big cats in zoos, both as native species in some countries and exotic in others, research on the attitudes of the general public towards their welfare and interactions with the public while in captivity is limited. This study explores attitudes of members of the public in India and Australia towards the welfare of big cats in captivity and identifies factors that contribute to their attitudes. The study was carried out using an online questionnaire which was shared via social media sites and by emailing zoo-associated organisations to share the links with its members. A total of 375 participants across the two countries completed the survey and the findings suggest that, overall, the number of zoo visits is a common factor influencing people's perspectives of captive big cats and their welfare. Other demographic factors such as location, age, gender and education, and the interactions between some of these factors, also influence perspectives. The findings emphasise the need to integrate socio-demographic factors in developing and accessing future zoo outreach programs for big cats according to their regions and consider targeting specific groups to enhance and broaden the public's understandings of big cats and their welfare.

Keywords: animal welfare, felids, human-animal interactions, perceptions**,** wild cats

5.2. Introduction

The field of animal welfare science has advanced and benefited from research in various multidisciplinary fields such as ethology, physiology, psychology, and sociology and shaped human-animal interactions (Lund, Coleman, Gunnarsson, Appleby, & Karkinen, 2006; Veissier & Miele, 2014). Whilst observing animals directly and using behavioural and physiological welfare indicators are important to measure their welfare, the further implementation of policies to safeguard their welfare depends on the role of society and human attitudes. Humans' attitudes towards animals are becoming increasingly important in animal welfare. Generally, people with positive attitudes towards preferred species are likely to show more care and concern towards their welfare, especially in response to judgments, decisions and behaviour that may underlie their concern (Kellert, 1985a; A. J. Knight, 2008; N. Taylor & Signal, 2005). Exploring human attitudes toward animals can therefore play a key role in understanding trends towards the welfare of animals (Cole & Fraser, 2018; Ward, Sherwen, & Clark, 2018). For example, recognizing that farm animals have sentience has promoted better regulations in raising livestock and improved farm animals' lives (Finkemeier et al., 2018). Similarly, being aware of the welfare requirements of wild animals such as endangered big cats in captivity may promote an interest in improving their lives. Past studies assessing humans' attitudes towards the welfare of wild animals have focused on zoo animals in general (De la Fuente, Souto, Caselli, & Schiel, 2018; Finlay, James, & Maple, 1988; Rhoads & Goldsworthy, 1979), including carnivores (Oražem, Majić Skrbinšek, Šorgo, & Tomažič, 2022), even though the welfare requirements may vary for a species or an individual animal.

Few studies have focused on attitudes towards the welfare of specific animals such as elephants (Gurusamy, Tribe, Toukhsati, & Phillips, 2015; Hacker & Miller, 2016), primates (Lukas & Ross, 2005), birds (Prokop, Kubiatko, & Fančovičová, 2008) and reptiles (Alves et al., 2012; Azevedo, Guimarães, Ferraz, Whiting, & Magalhães-Sant'Ana, 2022; Devlin & Ogle, 2022; Wolfe, Fleming, & Bateman, 2019). However, studies show that big cats, as charismatic megafauna, attract zoo visitors (Nyhus, Tilson, & Hutchins, 2010). While there are more big cats in captivity, such as tigers in

the U.S., than in the wild, few studies have assessed humans' attitudes towards the welfare of captive big cats in zoos. Among those, some have focused on specific stakeholder groups such as animal caretakers (Szokalski, 2014), zoo visitors (Cottle, Tamir, Hyseni, Bühler, & Lindemann-Matthies, 2010; Lund et al., 2006) and others (van der Meer, Botman, & Eckhardt, 2019), to report variations in attitudes. Stakeholders directly involved with ensuring the welfare of big cats play a significant role, but research on understanding the general public's perceptions towards their welfare is very limited. The responsibility of promoting big cat welfare to a wider audience is therefore necessary to better inform the public and other stakeholders' perceptions of ways to promote their welfare.

Understanding human attitudes is of crucial importance because the fulfilment of improvements for big cat welfare are greatly influenced by citizens' expectations (Vanhonacker, Verbeke, Van Poucke, & Tuyttens, 2008). Outreach and awareness programs on the past treatment of big cats in circuses and other private settings have informed some changes in policies and the management of big cats in captivity. They have also encouraged zoos to improve their role and proactively take on the responsibility of conservation centres to engage and educate visitors (Godinez & Fernandez, 2019; Skibins, Dunstan, & Pahlow, 2017). However, these changes may be slow to be implemented. More concerning, they may not be enough to promote the welfare of big cats in captivity, especially when comparing the lives of these big cats to their peers in the wild, and thus may be deemed unacceptable by some members of the public (Garner, 2021; Nyhus, Tilson, & Tomlinson, 2003). Therefore, with further scientific development in the field of big animal welfare, there is a need to align these findings with the attitudes and values of the public (Kirkwood & Hubrecht, 2001; Serpell, 2004).

In the zoos of India and Australia, big cats are managed as charismatic megafauna. In India, big cats are found in the wild, as well as managed in captivity. The Central Zoo Authority (CZA) is the governing body that develops guidelines for managing big cats in zoos, along with the responsibility of the individual state or territory for implementing these management policies (CZA, 2008). According to the latest CZA

inventory in 2020, 323 lions, 389 tigers, 579 leopards, 11 snow leopards, 14 jaguars and 2 cheetahs are in captivity across Indian zoos and rescue centres which are frequently visited by zoo visitors (CZA, 2020). The big cats in the rescue centres may have been abandoned as cubs or part of reintroduction breeding programs or are responsible for negative human-animal interactions in the past (Mathur, 2021; Vaz et al., 2017). Furthermore, some members of the Indian community may worship various big cats as deities (Athreya et al., 2018), some may coexist peacefully around the fringes of wildlife parks/sanctuaries while others may have had negative human-animal interactions (Athreya, Odden, Linnell, Krishnaswamy, & Karanth, 2013; Hathaway et al., 2017). Past research on the welfare of big cats in Indian zoos has focused on understanding animals' welfare through their physiology, behaviour, enrichment (Goswami et al., 2021; Vaz et al., 2017) and keepers' interactions (Narayan et al., 2017; Vaz et al., 2017). Some individuals of the community also volunteer in various research projects or in programs, such as Friends of Zoos (Mukherjee, Nandini, Karunakaran, & Khanolkar, 2021; Walker, 2012).

In Australia, big cats are managed only in captivity in zoos and rescue centres that have animals retired from zoos and circuses (RSPCA, 2021). The Zoo and Aquarium Association (ZAA) is responsible for regulating the policies around managing big cats in Australian zoos with individual zoos responsible for implementing the policies. Past research on the welfare of big cats in Australian zoos has focused on understanding animals' welfare through their physiology, behaviour, enrichment and keepers (Parnell et al., 2014; Vaz, Bartley, et al., 2022; Vaz, McElligott, et al., 2022). In general, the Australian community, is inclined towards programs involving donating to animal welfare groups, writing to newspapers, becoming a keeper for a day or other volunteering opportunities at zoos (Coleman, 2004; Ferguson, 2018; Tiplady, Walsh, & Phillips, 2013).

Close human-animal interactions or experiences have become a popular attraction in zoological institutions. Studies show that such interactions can have short-term and/or long-term impacts on human behaviours and perceptions (Learmonth, Chiew, Godinez, & Fernandez, 2021). In addition, portrayals of big cats in media

documentaries such as 'Big cats' (BBC One, 2018), sensational documentaries such as Tiger King (Bennett & Johnson, 2021) and/or news about the shutting down of the Tiger Temple have raised public awareness about the welfare of big cats (Cohen, 2019). Studies show that interacting closely with animals may be beneficial for all involved and may further generate pro-conservation behaviours or it may also lead to adverse effects among certain individuals for inappropriate wild-animal 'pet' ownership (Hosey, Melfi, & Ward, 2020; Learmonth, 2020). Some zoos allow close interactions with big cats. Although this may send mixed messages to the public and variously influence their perceptions, all avenues that can influence animal welfare policies and legislation at the societal level needs to be considered (Harcourt, Pennington, & Weber, 1986).

The Theory of Planned Behaviour (Ajzen, 1991) in animal welfare posits these human-animal interaction experiences may prompt individuals to advocate, support and actively contribute to animal conservation and/or animal initiatives. Thus, assessing the attitudes of the public is crucial, especially given the potential for them to act as a catalyst for animal welfare (Kellert, 1985a; Serpell, 2004). Further, human attitudes may be influenced by knowledge, beliefs, values, culture, animal interactions and wider societal experiences (Kellert, 1985a; Serpell, 2004; Sherwen & Hemsworth, 2019). Thus, it is important to consider various demographic measures such as location (Gurusamy et al., 2015), gender (Herzog, Betchart, & Pittman, 1991; Randler, Adan, et al., 2021), age (Randler, Ballouard, et al., 2021), education (Gurusamy et al., 2015; Teng, 2015) or other cultural aspects as they may act as driving factors affecting attitudes (Bowd & Bowd, 1989).

This study first explores the current attitudes of the public in India and Australia towards the welfare of big cats in captivity. Second, it identifies factors that contribute to the publics' attitudes. This study assesses similarities and/or differences in the publics' attitudes towards reasons for visiting zoos, the most liked aspects of big cats, preferred encounters with big cat management, preferred environmental conditions for big cats and any concerns for their welfare. It then examines if public perceptions can be predicted by considering the location, age, gender, education level, and number

of zoo visits of the public. Big cats are native to India; hence they are found both in the wild and in zoos and rescue centres. In Australia, big cats are only found in zoos, safari parks and rescue centres. Given this, we hypothesise there will be differences in public attitudes towards the welfare of big cats across the two countries. In both contexts, industry stakeholders and government authorities need to assess the perceptions, concerns, and attitudes of the public towards big cats to inform their approach to managing them. The findings of this study are thus important to make policymakers aware of public perceptions and for educators to promote resources to further educate the public about big cats and their welfare.

5.3. Methodology

5.3.1. Sampling design and respondents

A cross-sectional study was carried out using an online-based questionnaire to understand the current perceptions of members of the general public in both India and Australia towards the welfare of big cats in zoos (Figure 5.1). To encourage respondents over 18 years of age to participate in the survey, the questionnaire was distributed in two ways: a survey link was shared via social media sites such as Facebook, Twitter, Instagram, LinkedIn and WhatsApp; this link was also shared via email with zoo-associated organisations such as Australian Society of Zoo Keeping and the Zoo and Aquarium Association (ZAA) to circulate among the database of their members and visitors. Respondents received an information sheet about the study and the completion of the online questionnaire was taken as informed consent to participate. The questionnaire collected anonymous data from January to March 2022, and participants interested in receiving the results of the study were asked to leave their email addresses. Ethical approval was obtained from the Human Ethics Committee at Western Sydney University (H13741).

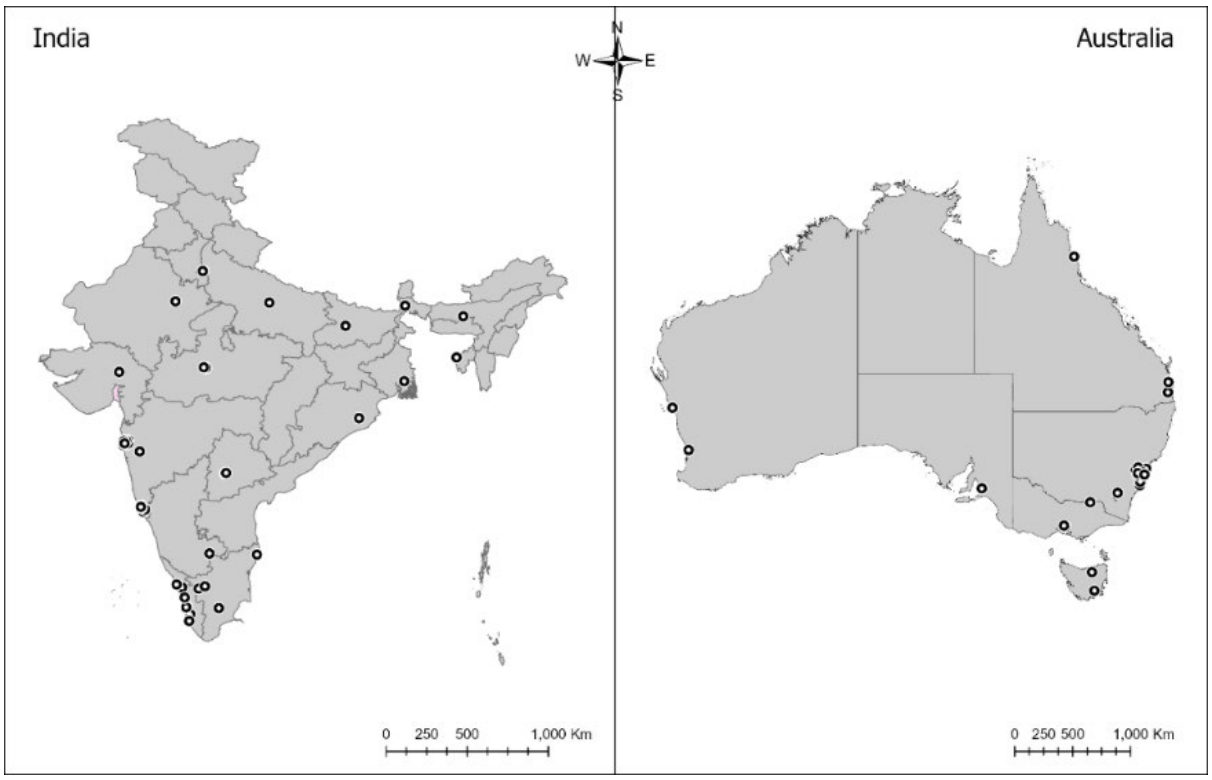

Figure 5. 1 Location of participants who participated in the study (n = 375) in India and Australia using ArcGIS Pro version 2.8.0

5.3.2. Questionnaire design

The online questionnaire was modified from a questionnaire on elephants and prepared on Qualtrics web-based software (Qualtrics LLC, Provo, Utah, USA) (Gurusamy et al., 2015). A pilot of the questionnaire was conducted with five participants in each country to assess its readability and comprehension. Minor modifications were made to the questionnaire to enhance its accessibility i.e., it was presented in two main sections (Table S5.1).

The first section consisted of seven questions that gathered participants' demographic information. The second section consisted of six constructs (Q1- Q6) with subscale questions using a Likert scale rating 1- 5, where 1 indicated "strongly disagree" and 5 indicated "strongly agree." These six constructs were concerned with reasons for visiting zoos (Q1), most liked aspects of big cats (Q2), encounters with big

cats (Q3), environmental conditions for big cats (Q4), big cat management (Q5) and big cat welfare (Q6).

5.3.3. Statistical analyses

The data from the questionnaire were analysed statistically analysis using SPSS version 27.0 (IBM Corp., Armonk, NY, USA). As the Likert scale rating was a multi-item measurement scale with a set of *k* items, its reliability needed to be considered (Coolican, 2014; Langdridge & Hagger-Johnson, 2013; Revicki, 2014). To test the internal consistency/reliability of the subscale items, we used the Cronbach's alpha (α) reliability coefficient for the six constructs (Cronbach, 1951; Tavakol & Dennick, 2011). The α coefficient value ranged between 0-1, where values closer to one indicated higher reliability and greater consistency of the items contained within the scale. Generally, values between 0.6-0.7 indicate an acceptable level of reliability, and 0.8 or greater is considered a very good level of reliability with subscales contributing to the constructs (Nunally, 1978; Ursachi, Horodnic, & Zait, 2015).

The demographic variables such as location, age, gender, education and number of zoo visits were used as independent fixed factors to identify which of these predicted respondents' attitudes towards big cats in captivity. Due to the non-normality in the data, General Linear Models (GLMs) were used to investigate and control for the effects of these demographic variables along with their interactions. The MANOVA model was first built using the main-effects along with all the 2-way, 3-way, 4-way and 5-way interactions between the demographic variables, with the significance level of the *P*-value set to 0.05. A stepwise progression from the maximal model through a series of simplifications to the minimal adequate model was made on the basis of backward elimination tests (Crawley, 1993). For instance, the complex model consisted of the main effects and all possible interactions; and a manual stepwise model simplification was then conducted by removing the least significant terms (largest *P*-value) first starting with the highest-order interactions (Cebrián-Piqueras et al., 2020; Pituch, 2015; Rexstad & Innis, 1985; Wongsaengchan &

McKeegan, 2019). This process was used to build the minimal adequate model that included the effects of all explanatory factors that were significantly different from zero ($P < 0.05$), and from one another, with all the non-significant explanatory variables removed (Cottle et al., 2010). Chi-squared tests were used to assess the significance of the increase in deviance, that resulted in a given term (variable or interaction of variables) being removed from each particular model. Alongside the multivariate analysis, a univariate analysis identified the significant multivariate terms to describe the overall difference between the groups. The Mean ± SE was calculated to understand the trends across the groups.

5.4. Results

5.4.1. Respondent's demographics

The questionnaire was completed by a total of 375 participants, with 168 (44.8%) respondents from Australia and 207 (55.2%) from India (Table 5.1). The age of participants ranged from 18 years to above 70 years, with women (63.20%) respondents outnumbering men (36.80%). Participants' education level varied: 37.3% held a master's degree or higher, 36.5% had completed a bachelor's degree, 14.7% had a diploma or trade degree, and 11.5% held a high-school degree or lower level of schooling. Of the 375 participants, 41.3% had visited zoos over 10 times, 25.9% had visited zoos between 5-10 times and 32.8% had visited zoos and other wildlife sanctuaries less than 5 times.

These participants either own or have owned pets (69.3%) compared to others (30.7%), and about 45.9% have children compared to others (54.1%). Of the respondents, 35.2% had worked with animals in the past and 85.9% indicated they were likely to visit a zoo in the future. This data were not used in this study.

Table 5. 1 Demography of participants according to country

Variables	Category	Australia	India	Total
Age	18-30 years	60	85	145
	31-40 years	37	38	75
	41-50 years	19	29	48
	51-60 years	25	32	57
	61-70 years and above	27	23	50
Gender	Male	44	94	138
	Female	124	113	237
Education	Grade 12 and below	20	23	43
	Diploma or Trade	46	9	55
	Bachelor's degree	55	82	137
	Master's Degree or higher	47	93	140
Past Zoo visits	< 5 times	43	80	123
	5-10 times	41	56	97
	> 10 times	84	71	155
Own/Owned pets	Yes	148	112	260
	No	20	95	115
Have children	Yes	76	96	172
	No	92	111	203
Working/Worked with animals	Yes	77	55	132
	No	91	152	243
May visit a zoo in the future	Yes	151	171	322
	No	17	36	53

5.4.2. Reliability and construct validity

The reliability of participants' responses using Cronbach's α, as depicted in Table 5.2, was found to be highly reliable for Q2, Q3 and Q5, and moderately acceptable values for Q1 and Q4. These results indicate that these five questions all contributed strongly to the construct, while Q6 was found to have low reliability. As the reliability test does not affect the multivariate analysis, Q6 was included in further analyses.

Table 5. 2 Reliability measure using Cronbach's alpha (α)

Construct questions	Cronbach's α
Q1 - Reasons for visiting zoos	0.676*
Q2 - Most liked aspects of big cats	0.783*
Q3 - Encounters with big cats	0.876**
Q4 - Environmental conditions for big cats	0.666*
Q5 - Interactions with big cat management	0.847**
Q6- Big cat welfare concerns	0.389

*Values between 0.6-0.7 indicate moderate or acceptable level of reliability, and **0.8 or greater values indicate a high reliability with subscales contributing to the constructs

5.4.3. Potential factors influencing perceptions towards big cats and their welfare

5.4.3.1. Reasons for visiting zoos

The overall MANOVA model revealed significant multivariate effects for age, gender and zoo visits as main effects on the reasons for visiting zoos; the resulting model also contained the two-way interaction terms (L X A) (Table 5.3).

Table 5. 3 Overall Generalized Linear Model -MANOVA examining the reasons for visiting zoos with the demographic variables and their interactions as factors. The model represents a minimal adequate model.

Model terms	MANOVA			
	Pillai's Trace	df	*F*	*P*
Location (L)	0.033	6, 354	2.023	0.062
Age (A)	0.112	24, 1428	1.714	**0.017**
Gender (G)	0.078	6, 354	4.959	**0.000**
Education (E)	0.065	18, 1068	1.308	0.174
Zoo visits (Z)	0.080	12, 710	2.454	**0.004**
L X A	0.119	24, 1428	1.818	**0.009**

'X' represents an interaction between independent variables. Boldface represents a significant difference (P = <0.05)

There were significant differences between the age groups in their reasons for visiting zoos. The univariate analyses revealed that spending time with family was a strong reason among the age group 61 years and above (4.3 ± 0.134), followed by the 31- 40 years (4.27 ± 0.127), 41- 50 years (3.96 ± 0.178), 18 - 30 years (3.91 ± 0.096) and 51- 60

years (3.86 ± 0.179) (Table S5.2). There were also significant differences in gender for learning about big cat conservation, with a higher interest in females (4.26 ± 0.059) than males (3.93 ± 0.102). There were significant differences in attitudes towards seeing rare and endangered animals such as big cats, which varied with zoo visits and was higher among individuals who visited the zoo >10 times (4.08 ± 0.093), followed by others who visited 5-10 times (3.81 ± 0.109) and lastly among those < 5 times (3.40 ± 0.122). Seeing rare and endangered big cats, being entertained, or impressed by big cats and learning about big cat conservation were further influenced by the combined effect of (L X A) (Figure 5.2).

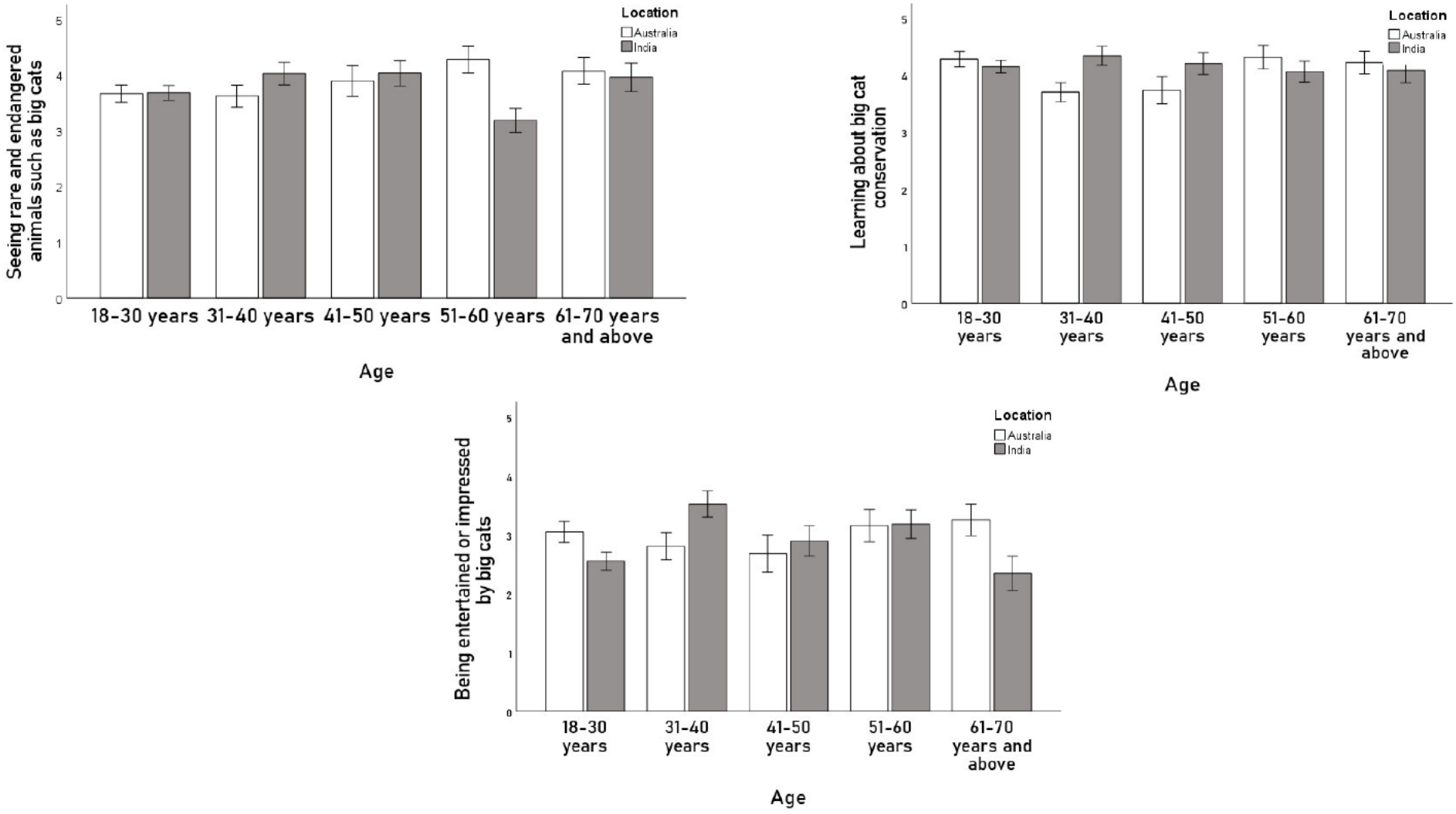

Figure 5. 2 The effect of two-way interactions on the reasons for visiting zoos

5.4.3.2. Most liked aspects of big cats

The overall MANOVA model revealed location, gender and zoo visits as main effects influencing the most liked aspects of big cats, with the resulting model containing the two-way interaction terms (G X E) and (A X Z) (Table 5.4).

Table 5. 4 Overall Generalized Linear Model -MANOVA examining the most liked aspects of big cats with the demographic variables and their interactions as factors. The model represents a minimal adequate model.

	MANOVA			
Model terms	**Pillai's Trace**	**df**	***F***	***P***
Location (L)	0.094	8, 345	4.5	**0.00**
Age (A)	0.106	32, 1392	1.189	0.217
Gender (G)	0.045	8, 345	2.034	**0.042**
Education (E)	0.052	24, 1041	0.76	0.79
Zoo visits (Z)	0.088	16, 692	1.982	**0.012**
G X E	0.108	24, 1041	1.624	**0.03**
A X Z	0.25	64, 2816	1.421	**0.016**

'X' represents an interaction between independent variables. Boldface represents a significant difference (P = <0.05)

There were significant differences between India and Australia in the most liked aspects of big cats, with the univariate analyses revealing Indian participants showed higher levels of likeness towards colours/coat patterns (4.30 ± 0.062), size (4.22 ± 0.293), unique feline/ cat behaviours (4.28 ± 0.297) and roar/purr of big cats (4.02 ± 0.075) than Australians: colours/coat patterns (3.89 ± 0.067), size (3.96 ± 0.305), unique feline/ cat behaviours (4.10 ± 0.315), and roar/purr of big cats (3.67 ± 0.082) respectively (Table S5.3). There were also significant gender differences across both countries towards unique feline/ cat behaviours, with a higher interest in females (4.25 ± 0.056) than males (4.10 ± 0.071). Preferences for colours/coat patterns were higher among individuals who visited the zoo >10 times (4.26 ± 0.069), followed by 5-10 times (4.04 ± 0.097), < 5 times (4.01 ± 0.082). Similarly, preferences for hunting skills were higher among individuals who visited the zoo >10 times (4.11 ± 0.084), followed by 5-10 times (3.70 ± 0.139) and < 5 times (3.64 ± 0.128). A similar trend was also seen for unique feline/ cat behaviours among individuals who visited the zoo >10 times (4.35 ± 0.06), followed by 5-10 times (4.14 ± 0.084), < 5 times (4.05 ± 0.07). However,

with regard to the whole animal as a liked aspect of big cats, individuals who visited the zoo >10 times (4.53 ± 0.065) showed more interest than those who visited < 5 times (4.31 ± 0.074) and 5-10 times (4.27 ± 0.093). Lastly, there was a significant effect of interaction terms (G X E) towards unique feline/ cat behaviours and the whole animal, and a significant effect of (A X Z) towards hunting skills, unique feline/ cat behaviours and cubs (Figure 5.3).

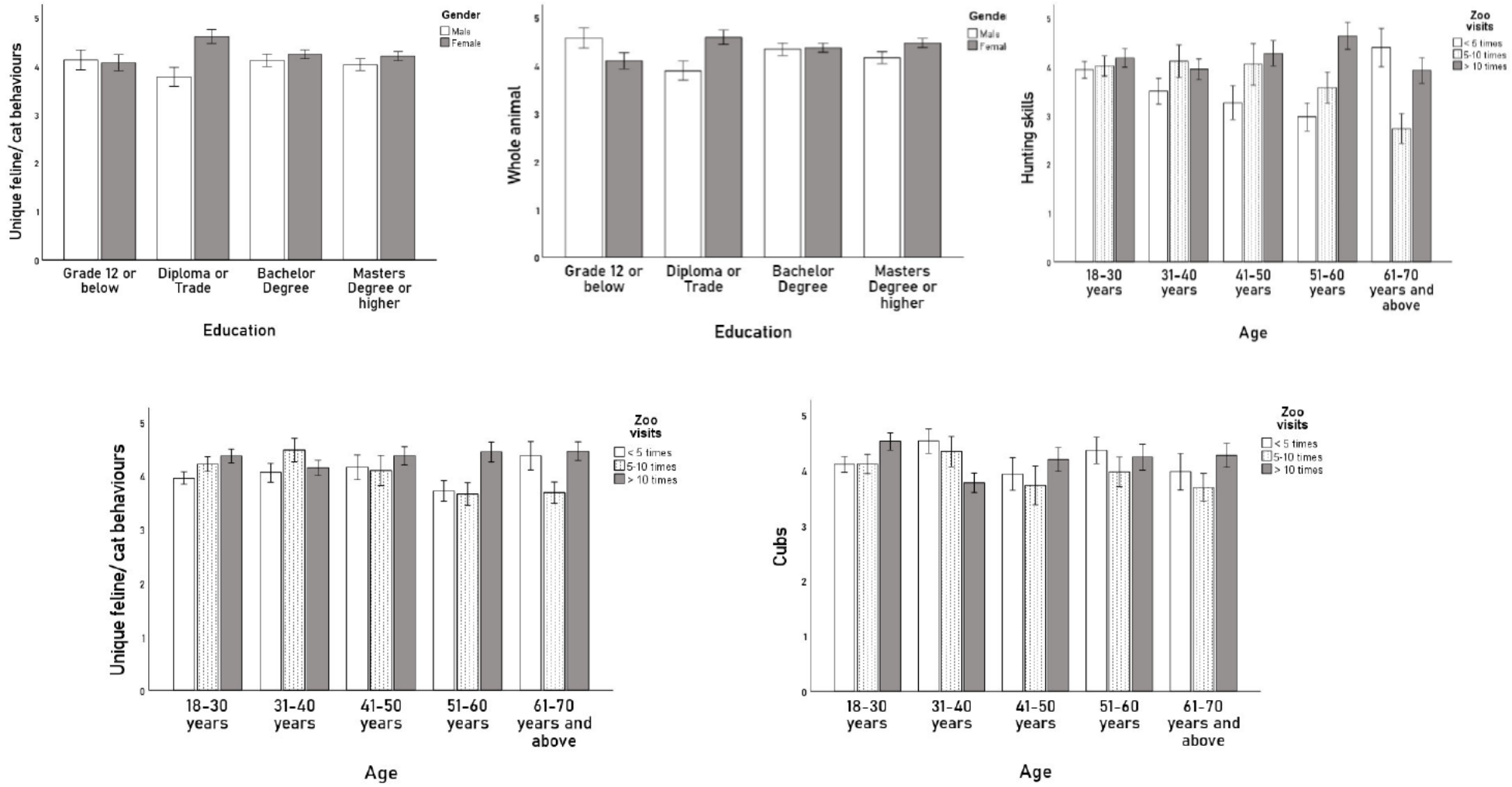

Figure 5. 3 The effect of two-way interactions on the most liked aspects of big cats

5.4.3.3. Encounters with big cats

The overall MANOVA model revealed significant multivariate effects of location, age and zoo visits as main effects towards encounters with big cats with the resulting model containing the three-way interaction term (A X G X E) (Table 5.5).

Table 5. 5 Overall Generalized Linear Model - MANOVA examining the encounters with big cats along with the demographic variables and their interactions as factors. The model represents a minimal adequate model.

	MANOVA			
Model terms	**Pillai's Trace**	**df**	***F***	***P***
Location (L)	0.166	8, 325	8.091	**0.000**
Age (A)	0.139	32, 1312	1.480	**0.042**
Gender (G)	0.015	8, 325	0.605	0.773
Education (E)	0.082	24, 981	1.148	0.282
Zoo visits (Z)	0.121	16, 652	2.621	**0.001**
A X G X E	0.836	248, 2656	1.250	**0.007**

'X' represents an interaction between independent variables. Boldface represents a significant difference (P = <0.05)

There were significant differences between the participants in the two countries towards views about encounters with big cats. The univariate analyses revealed that India (1.96 ± 0.945) showed more disagreement to visitors feeding big cats than Australia (2.32 ± 0.859), while Australia (1.65 ± 0.076) disagreed more on playing with big cats or their cubs than India (2.01 ± 0.096) (Table S5.4). Australia (3.04 ± 0.102) showed more neutral views towards visitors being allowed behind the scenes for a closer look of big cats while there was more disagreement in Indian (2.59 ± 0.106). Australia (4.02 ± 0.070) showed a higher level of interest for live video streaming of big cats in zoos, rescue centres than India (3.48 ± 0.093). Further, there were significant differences in views about visitors being allowed to walk with big cats which varied with age: 31-40 years (2.33 ± 0.106), 41-50 years (2.10 ± 0.188), 18-30 years (2.03 ± 0.106) somewhat disagreed while 51-60 years (1.88 ± 0.158) and 61 years and above (1.86 ± 0.153) respectively strongly disagreed. The views about visitors feeding big cats also varied with somewhat disagreeing views among 31-40 years (2.43 ± 0.176), followed by 18-30 years (2.17 ± 0.108), 41-50 years (2.06 ± 0.200), while 51-60 years (1.93 ± 0.160),

and 61 years and above (1.80 ± 0.145) were strongly disagreeing. Similarly, participants' views about visitors posing with big cats or their cubs were diverse and somewhat disagreed by 31-40 years (2.09 ± 0.167), 41-50 years (2.04 ± 0.206), and strongly disagreed by 18-30 years (1.82 ± 0.095), 51-60 years (1.70 ± 0.143) and 61 years and above (1.62 ± 0.148). In addition, visitors allowed behind the scenes for a closer look of big cats was viewed neutral by participants who have visited the zoo > 10 times (3.06 ± 0.118), followed by somewhat disagreement for those who visited < 5 times (2.71 ± 0.125) and others who visited between 5-10 times (2.46 ± 0.149). Regarding views about using safari buses by visitors to view big cats in safari parks, large zoo enclosures; a higher interest was seen among individuals who visited the zoo > 10 times (4.01 ± 0.074), followed by those who visited 5-10 times (3.81 ± 0.103) and < 5 times (3.61 ± 0.105). Similarly, for live video streaming of big cats in zoos, rescue centres, the views were highest among individuals who visited the zoo > 10 times (4.06 ± 0.085), followed by those who visited 5-10 times (3.52 ± 0.124) and < 5 times (3.45 ± 0.111). Lastly, there is a significant effect of the three-way interaction (A X G X E) on the views about visitors allowed to walk with big cats, visitors posing with big cats or their cubs and selfies with big cats (Figure 5.4).

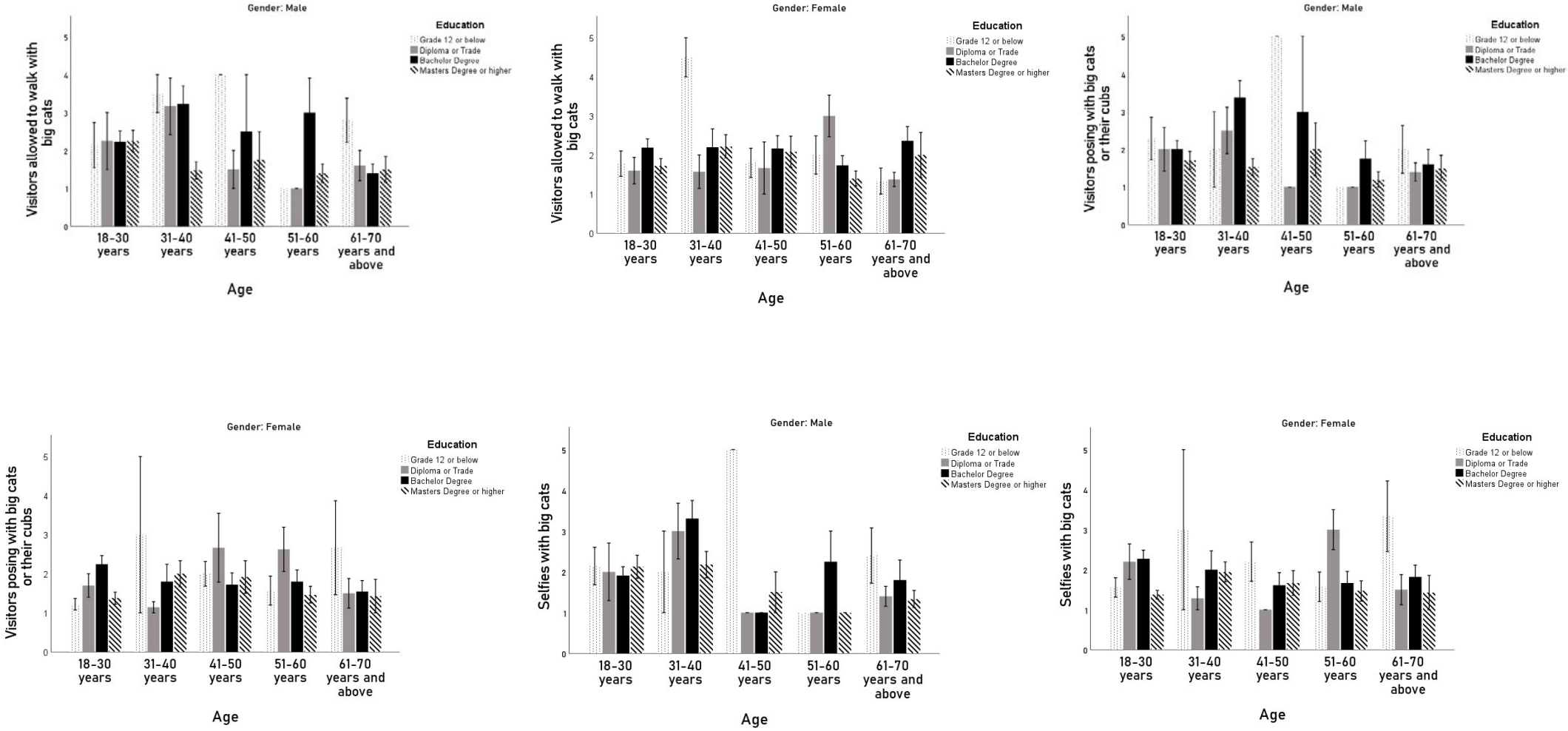

Figure 5. 4 The effect of three-way interactions on the views about encounters with big cats

5.4.3.4. Environmental conditions preferred for big cats

The overall MANOVA model revealed significant multivariate effects of location, age and zoo visits as main effects towards environmental conditions preferred for big cats and the resulting model also contained the two-way interaction terms (L X E), (A X G), (A X Z), and three-way interaction term (L X E X Z) (Table 5.6).

Table 5. 6 Overall Generalized Linear Model - MANOVA examining the environmental conditions preferred for big cats with the demographic variables and their interactions as factors. The model constructed was a minimal adequate model.

	MANOVA			
Model terms	**Pillai's Trace**	**df**	***F***	***P***
Location (L)	0.145	8, 327	6.924	**0.000**
Age (A)	0.140	32, 1320	1.497	**0.038**
Gender (G)	0.038	8, 327	1.612	0.120
Education (E)	0.084	24, 987	1.183	0.247
Zoo visits (Z)	0.117	16, 656	2.544	**0.001**
L X E	0.117	24, 987	1.669	**0.023**
A X G	0.139	24, 1320	1.480	**0.042**
A X Z	0.289	96, 2672	1.564	**0.003**
L X E X Z	0.407	112, 2672	1.279	**0.028**

'X' represents an interaction between independent variables. Boldface represents a significant difference (P = <0.05)

There were significant differences between the two countries towards environmental conditions preferred for big cats. The univariate analyses revealed that Australia (4.24 ± 0.081) showed a higher preference for enrichment items in the enclosure for big cats than India (3.29 ± 0.107) (Table S5.5). Australia (4.61 ± 0.049) also preferred animals to be kept in social groups rather than solitary animals which was preferred than India (3.84 ± 0.088). Further, Australia (4.78 ± 0.040) preferred big cat enclosures to include hiding spots for big cats to rest and have privacy (which may hide them from view for visitors) slightly more than India (4.57 ± 0.054), and Australia (4.71 ± 0.047) also preferred having enough space between different cat enclosures than the Indian public (4.59 ± 0.0459).

Age was a factor in participants' preferences of enrichment items in the enclosure for big cats. Participants from 31-40 years (3.92 ± 0.156), followed by 18-30 years (3.90 ± 0.115), 61-70 years (3.68 ± 0.198), 41-50 years (3.48 ± 0.220) and 51-60 years (3.21 ± 0.191) respectively showed somewhat agreement for enrichment items. Preferences for animals to be kept in social groups over solitary animals varied strongly for 61-70 years old (4.38 ± 0.150), 18-30 years old (4.30 ± 0.081), 31-40 years old (4.07 ± 0.141), 51-60 years old (4.05 ± 0.140) and 41-50 years old (3.98 ± 0.189) respectively. In addition, there were significant differences in preferences for enrichment items in the enclosure for big cats, which was highest among those that visited the zoo > 10 times (4.15 ± 0.100), followed by 5-10 times (3.45 ± 0.150) and < 5 times (3.37 ± 0.131324857) respectively; similarly the preferences for animals to be kept in social groups over solitary animals was higher among those who visited > 10 times (4.51 ± 0.069), followed by 5-10 times (4.07 ± 0.111) and < 5 times (3.86 ± 0.114) respectively. The preference for providing hiding spots in enclosures for big cats to rest and have privacy was higher among those who visited a zoo > 10 times (4.87 ± 0.029), < 5 times (4.52 ± 0.073) times and 5-10 times (4.51 ± 0.083) respectively; and having enough space between different cat enclosures was highest seen in respondents who visited a zoo > 10 times (4.73 ± 0.048), 5-10 times (4.65 ± 0.068) and < 5 times (4.54 ± 0.058) respectively. Additionally, there was a significant effect of (L X E) towards the preferences for animals to be kept in social groups over solitary animals alone and enough space between different cat enclosures. Although overall there was a significant effect of the interaction term (A X G) on environmental preferences, it was not seen individually in the univariates. There was also a significant effect of (A X Z) on preferences for hiding spots for big cats to rest and have privacy. Lastly, a significant effect of three-way interaction (L X E X Z) was seen in the preference for animals to be kept in social groups (such as lions in a pride) and solitary animals (such as tigers) to be alone and to provide hiding spots for big cats to rest and have privacy (which may not be visible to visitors) (Figure 5.5).

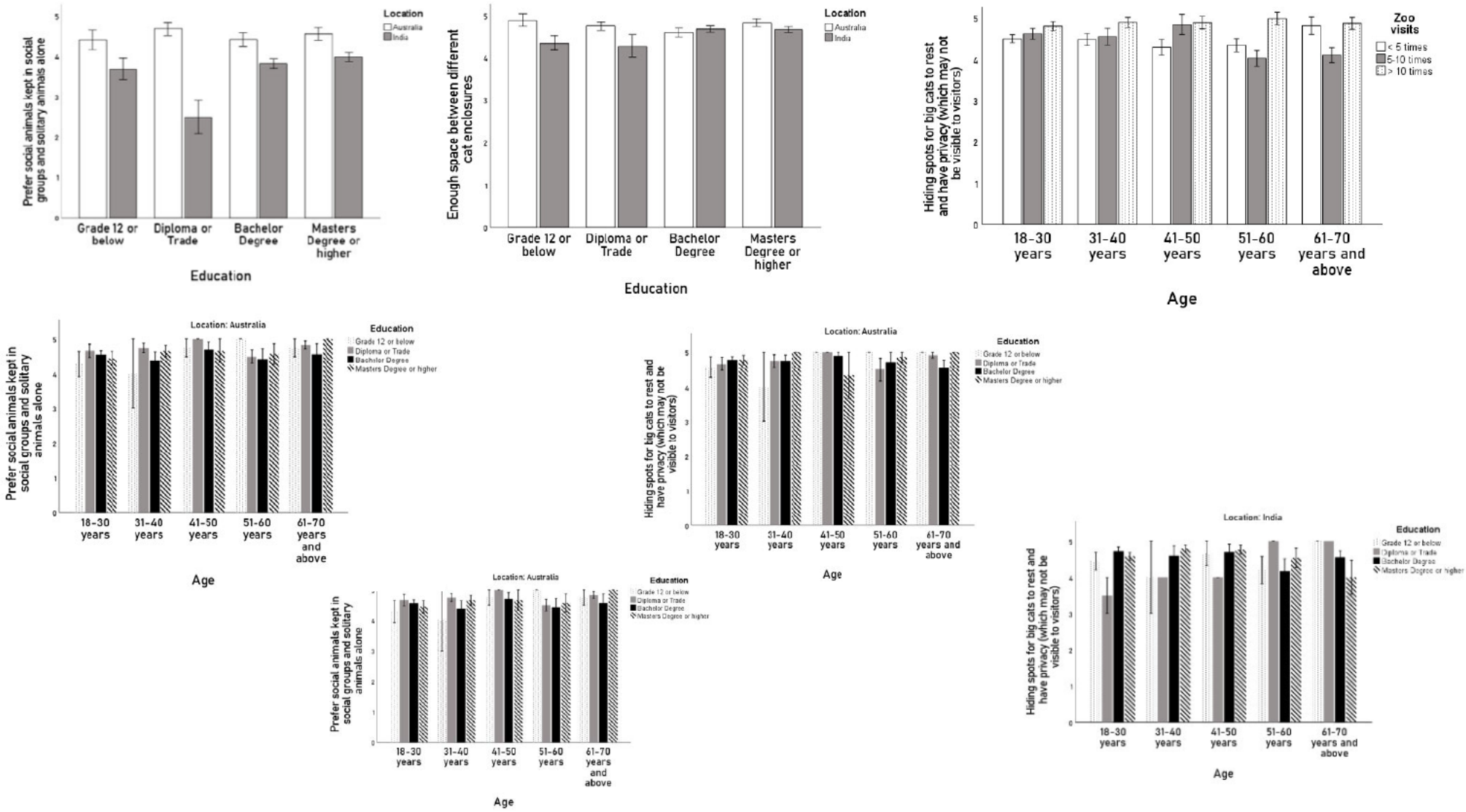

Figure 5. 5 The effect of two and three-way interactions on the environmental conditions for big cats

5.4.3.5. Interactions with big cat management

The overall MANOVA model revealed significant multivariate effects of location and zoo visits as main effects towards interactions with big cat management, and the resulting model also contained the two-way interaction terms (A X E), (L X A), (A X G), (G X Z), (A X Z) and three-way interaction term (A X G X E) (Table 5.7).

Table 5. 7 Overall Generalized Linear Model - MANOVA examining the interactions with big cat management along with the demographic variables and their interactions as factors. The model represents a minimal adequate model.

	MANOVA			
Model terms	**Pillai's Trace**	**df**	***F***	***P***
Location (L)	0.093	8, 311	3.987	**0.000**
Age (A)	0.116	32, 1256	1.177	0.230
Gender (G)	0.034	8, 311	1.362	0.213
Education (E)	0.070	24, 939	0.941	0.544
Zoo visits (Z)	0.157	16, 624	3.325	**0.000**
A X E	0.387	96, 2544	1.346	**0.015**
L X A	0.158	32, 1256	1.617	**0.017**
A X G	0.219	32, 1256	2.275	**0.000**
G X Z	0.136	16, 624	2.842	**0.000**
A X Z	0.315	64, 2544	1.631	**0.001**
A X G X E	0.486	120, 2544	1.372	**0.005**

'X' represents an interaction between independent variables. Boldface represents a significant difference (P = <0.05)

There were significant differences between the two countries towards interactions with big cat management, and the univariate analyses revealed that India showed a higher interest in partnering with zoos for CSR (Corporate Social Responsibility) activities (4.22 ± 0.061) than Australia (3.75 ± 0.076), undertaking fundraising events for rescued big cats (e.g., bake, art or photograph sale, etc.) (4.27 ± 0.064) than Australia (3.72 ± 0.083), and donating to zoos' partnerships to support big cats in the wild (4.37 ± 0.055) than Australia (3.92 ± 0.083) (Table S5.6). There was also a significant difference in attitudes towards attending keeper talks as seen highest among those who visited zoos > 10 times (4.56 ± 0.059), followed by 5-10 times (4.08 ± 0.081) and < 5 times (4.04 ± 0.076); for visiting the animal hospital at the zoo if permitted, the views

were highest among those who visited > 10 times (3.99 ± 0.091) followed by < 5 times (3.62 ± 0.104) and 5-10 times (3.53 ± 0.124). Additionally, for participating in research/volunteering opportunities at zoo, was highest among those who visited > 10 times (4.39 ± 0.070), followed by 5-10 times (4.11 ± 0.103) and < 5 times (3.97 ± 0.099). Similarly, for talking to keepers about their big cat's well-being was seen highest among visitors who visited zoos > 10 times (4.50 ± 0.061) followed by 5-10 times (4.31 ± 0.078) and < 5 times (4.20 ± 0.087) and for buying gift certificates to adopt rescued/injured big cats was highest among visitors who visited zoos > 10 times (4.01 ± 0.087) followed by 5-10 times (3.66 ± 0.122) and < 5 times (3.64 ± 0.113). The positive attitude for donating to zoos' partnerships to support big cats in the wild seen highest among those who visited > 10 times (4.32 ± 0.076), followed by < 5 times (4.10 ± 0.085) and then the 5-10 times (4.02 ± 0.098). Although overall there was a significant effect of the interaction terms (A X E) and (L X A), it was not seen individually. In addition, there is a significant effect of (A X G) on attending keeper talks, participating in research/volunteering opportunities at zoo, buying gift certificates to adopt rescued/injured big cats, partnering with zoos for CSR projects, undertaking fundraising events for rescued big cats (e.g., bake, art or photograph sale, etc.) and donating to zoos' partnerships to support big cats in the wild (Figure 5.6). There was also a significant effect of (G X Z) on talking to keepers about their big cat's well-being and donating to zoos' partnerships to support big cats in the wild. Further, there was a significant effect of (A X Z) on talking to keepers about their big cat's well-being, undertaking fundraising events for rescued big cats (e.g., bake, art, or photograph sale, etc.) and donating to zoos' partnerships to support big cats in the wild (Figure 5.7). Lastly, a significant effect of three-way interaction (A X G X E) was also seen in buying gift certificates to adopt rescued/injured big cats (Figure 5.8).

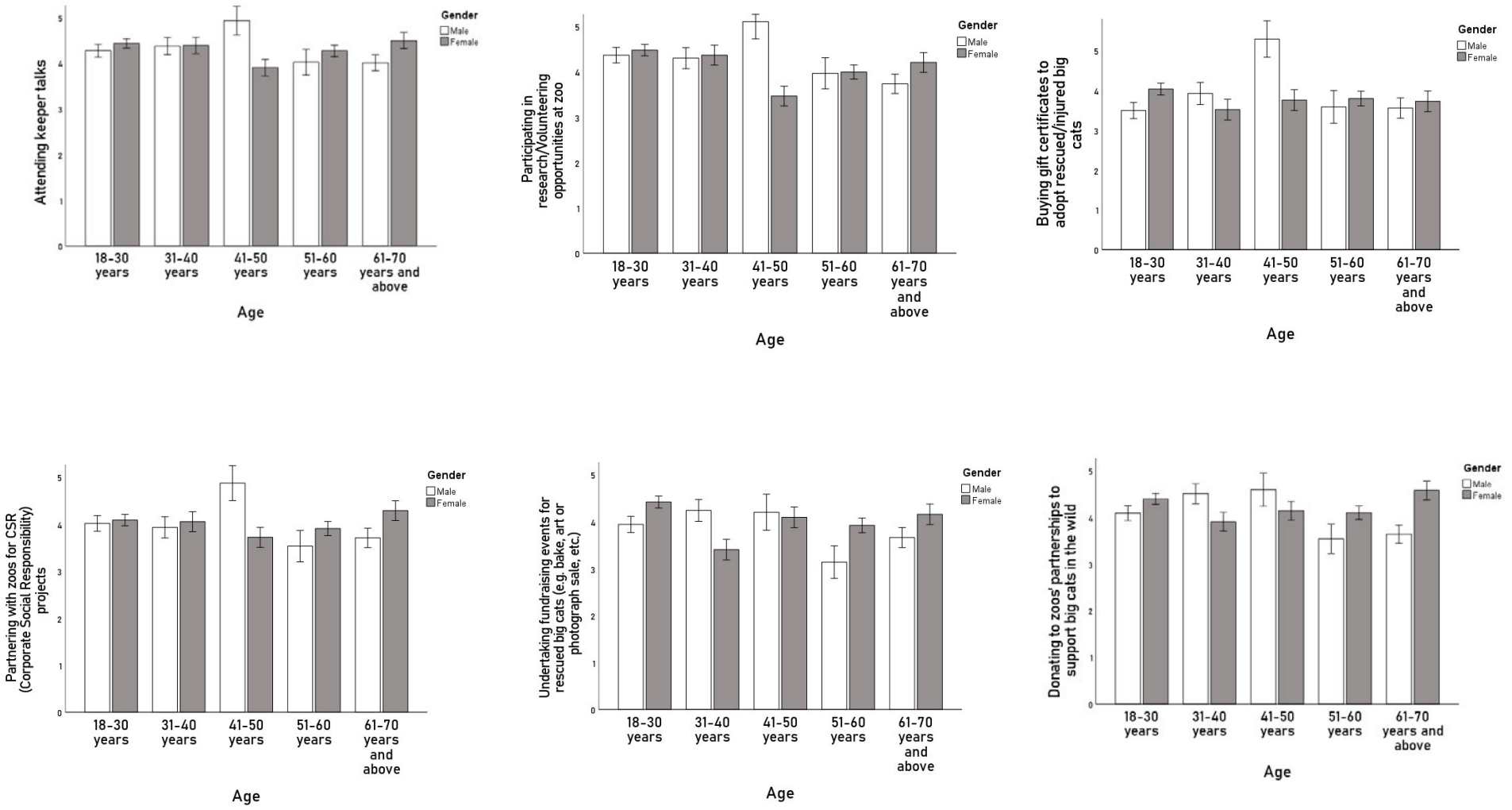

Figure 5. 6 The effect of two-way interactions on the interactions with big cat management

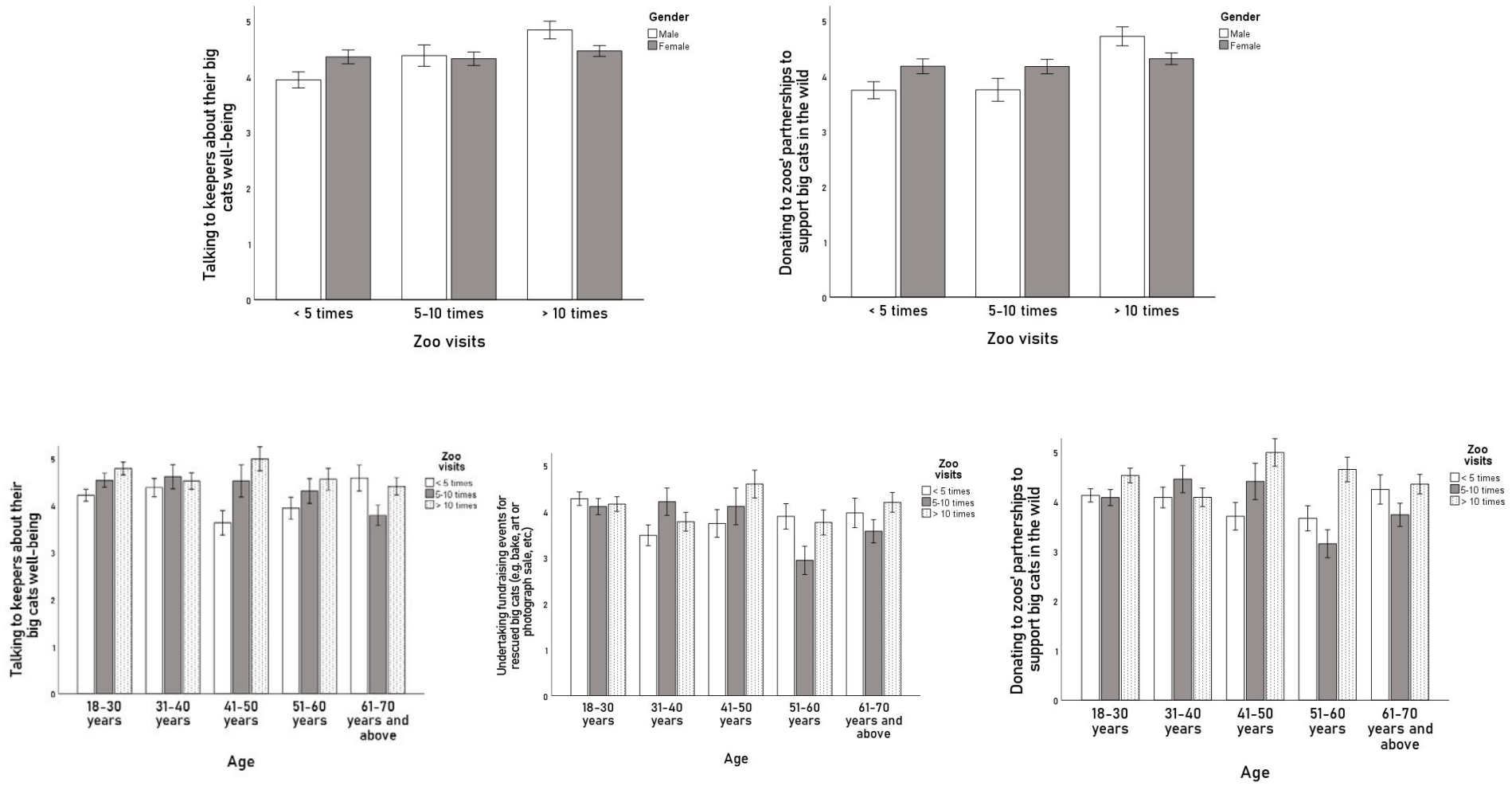

Figure 5. 7 The effect of two-way interactions on the interactions with big cat management

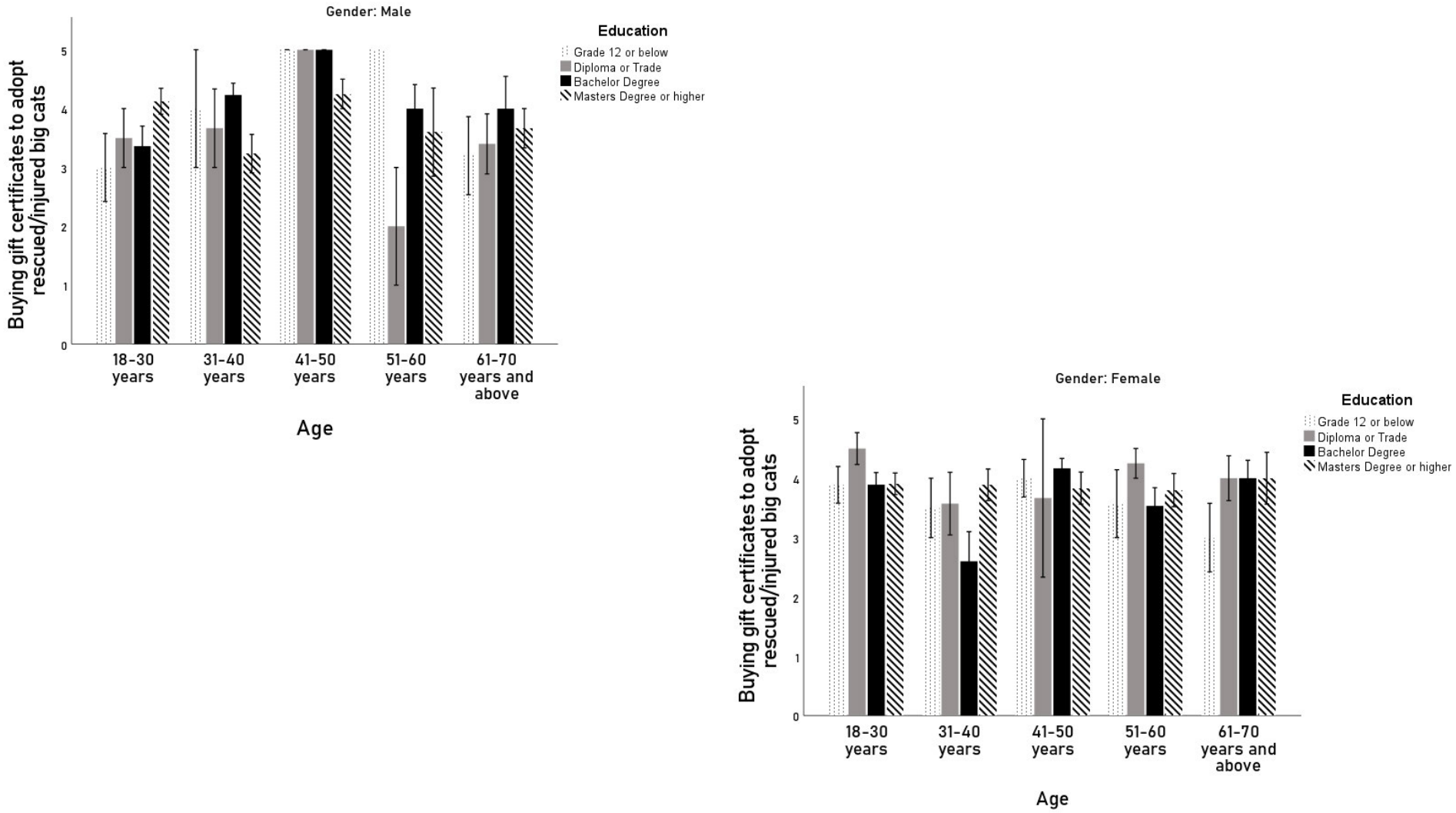

Figure 5. 8 The effect of three-way interactions on the interactions with big cat management

5.4.3.6. Big cat welfare concerns

The overall MANOVA model revealed significant multivariate effects of location, age, gender and zoo visits as main effects towards the big cat welfare concerns, and the resulting model also contained the two-way interaction term (L X Z) (Table 5.8).

Table 5. 8 Overall Generalized Linear Model - MANOVA examining the big cat welfare concerns with the demographic variables and their interactions as factors. The model represents a minimal adequate model.

	MANOVA			
Model terms	**Pillai's Trace**	**df**	***F***	***P***
Location (L)	0.168	8, 354	8.935	**0.000**
Age (A)	0.131	32, 1428	1.506	**0.035**
Gender (G)	0.059	8, 354	2.749	**0.006**
Education (E)	0.064	24, 1068	0.963	0.513
Zoo visits (Z)	0.154	16, 710	3.704	**0.000**
L X Z	0.097	16, 710	2.268	**0.003**

'X' represents an interaction between independent variables. Boldface represents a significant difference (P = <0.05)

There were significant differences between the two countries towards big cat welfare concerns, and the univariate analyses revealed that India (3.29 ± 0.094) showed more neutral views towards feeding live prey to big cats (such as live deer, pig, etc.) while Australia (2.68 ± 0.100) showed somewhat disagreement (Table S5.7). India (4.38 ± 0.068) showed more agreement than Australia (3.61 ± 0.095) towards breeding of big cats should only be for reintroduction to the wild and not for zoos and private owners, while Australian public (3.86 ± 0.091) showed higher views towards having old or injured big cats (e.g., missing a limb) in zoos than people in India (3.27 ± 0.100). Also, the Indian public (3.85 ± 0.081) showed higher interest than Australia (3.00 ± 0.097) towards big cats being bred in their native country for the purpose of conservation. Further, there was also a significant difference in attitudes according to age groups towards feeding live prey to big cats (such as live deer, pig, etc.) with more neutral views among age groups 41-50 years (3.38 ± 0.192), followed by 18-30 years (3.23 ± 0.109), somewhat negative views by 31-40 years (2.91 ± 0.166), 51-60 years (2.70 ± 0.173), 61-70 years and above (2.60 ± 0.182). For private ownership of big cats, strong

disagreement was seen among 41-50 years (1.88 ± 0.187), 31-40 years (1.85 ± 0.139), 18-30 years (1.72 ± 0.096), 51-60 years (1.44 ± 0.114), 61-70 years and above (1.30 ± 0.095).

Additionally, we found a significant effect of gender on selective breeding of big cats such as white tigers affect big cat conservation negatively with females (4.08 ± 0.064) showing a higher concern than males (3.81 ± 0.097). Females (2.15 ± 0.082) had lower disagreed views on killing of big cats involved in negative incidents/encounters/attacks as compared to males (2.58 ± 0.125); and females (3.67 ± 0.086) were more neutral towards having old or injured big cats (e.g., missing a limb) in zoos than males (3.30 ± 0.118). In addition, the differences in views towards breeding of big cats should only be for reintroduction to the wild and not for zoos and private owners was seen higher among those who visited the zoo < 5 times (4.35 ± 0.087), 5-10 times (4.01 ± 0.107) and > 10 times (3.80 ± 0.105). While considering views about boredom affecting big cats, it was seen higher among those that visited the zoo > 10 times (4.50 ± 0.062), < 5 times (4.20 ± 0.076), 5-10 times (4.15 ± 0.101). However, there were somewhat disagreed views towards killing of big cats involved in negative incidents/encounters/attacks which was higher among those that visited the zoos > 10 times (2.24 ± 0.110), < 5 times (2.54 ± 0.128), 5-10 times (2.11 ± 0.123). Further there were neutral views towards having old or injured big cats (e.g., missing a limb) in zoos, which was higher among those that visited the zoo > 10 times (3.92 ± 0.097), 5-10 times (3.31 ± 0.146) and < 5 times (3.24 ± 0.125).

There were neutral views about big cats being bred in their native country only for the purpose of conservation, which was higher among those who visited the zoo < 5 times (3.76 ± 0.100), 5-10 times (3.54 ± 0.128) and > 10 times (3.20 ± 0.109). Lastly, the effect of (L X Z), had a significant difference in views on feeding live prey to big cats (such as live deer, pig, etc.), breeding of big cats should only be for reintroduction to the wild and not for zoos and private owners, killing of big cats involved in negative incidents/encounters/attacks and big cats should only be bred in their native country for the purpose of conservation (Figure 5.9).

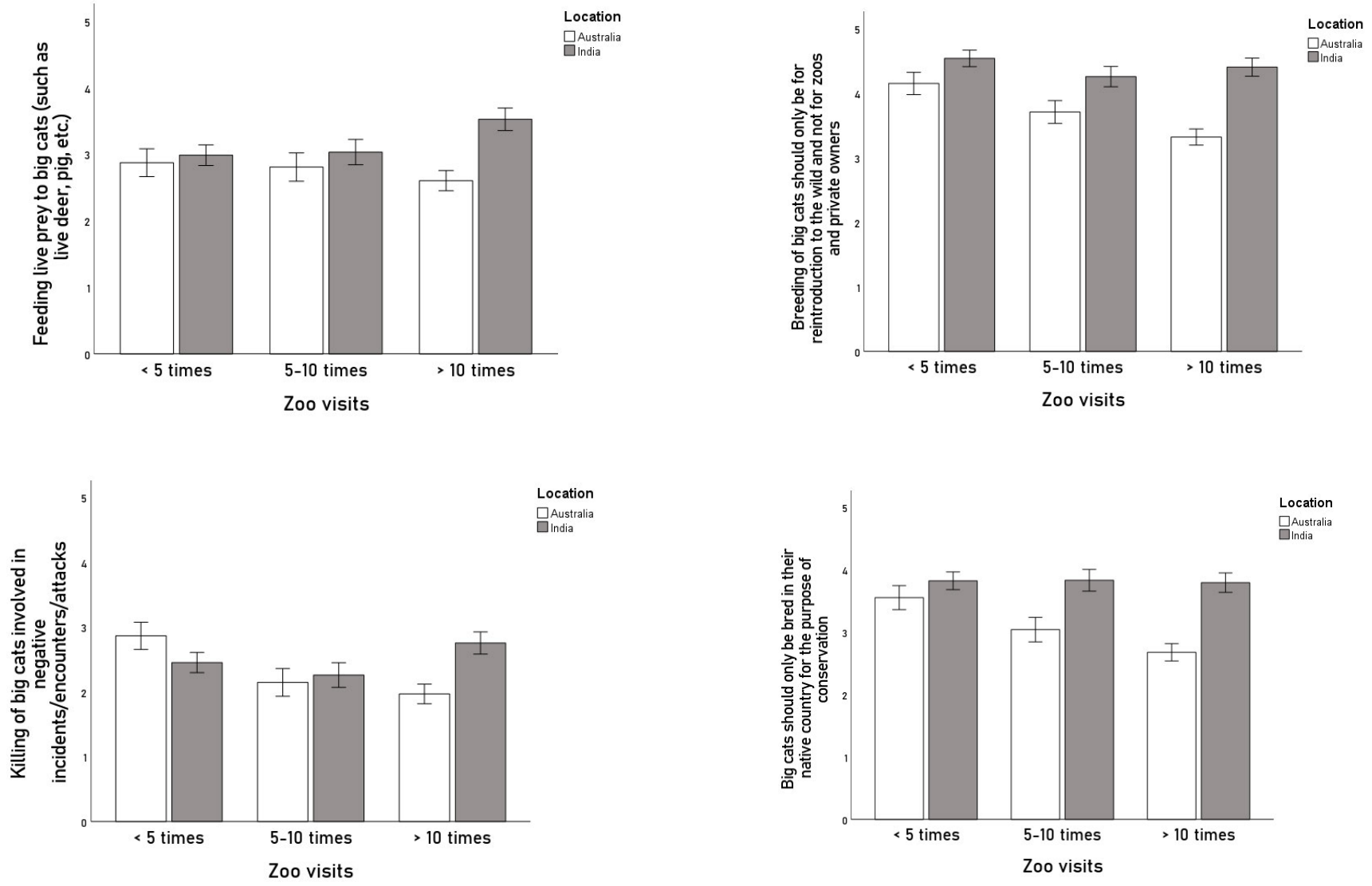

Figure 5. 9 The effect of two-way interactions on the big cat welfare concerns

5.5. Discussion

This study assessed the current attitudes of the Indian and Australian public towards captive big cats and their welfare, and explored factors that may influence these attitudes. Our study specifically assessed if there were differences in participants' reasons for visiting zoos, the most liked aspects of big cats, preferred encounters with big cat management, preferred environmental conditions for big cats and big cat welfare concerns. We assessed if these attitudes could be predicted by participants' location, age, gender, education, and past number of zoo visits. The results confirmed most of our predictions, with some differences from previous research. For example, overall, we found the number of zoo visits was strongly associated with all six constructs used for measuring attitudes towards big cats and their welfare. In addition, the results revealed how the subscales under each construct were influenced by different factors. While previous studies have regularly viewed the publics' perceptions and attitudes to big cats and their welfare be distinct due to the influence of various factors (Kellert, 1985a), our results show a high level of association between the interactions and the factors, as detailed below.

5.5.1. Factors influencing attitudes towards captive big cats and their welfare

One of the main aims of this study was to assess how participants from different countries perceive the welfare of big cats in zoos. The general public in India held more fascination towards big cats for their appearance, size, feline behaviours and roar; and this may be explained by the accessibility and closeness to a variety of wild cats in Indian zoos (CZA, 2020). Cultural similarities and differences tied to religion, closeness to animals, past philosophies concerning animals remain the focus of interest for a society and an ethical issue (Bruder et al., 2022; Szűcs, Geers, Jezierski, Sossidou, & Broom, 2012). However, participants from both countries showed varying levels of disagreement towards visitors feeding and playing with big cats or cubs, but a more positive interest in live video streaming for big cats in zoos. This may indicate a growing awareness about the past treatment of captive big cats through social media

and welfare activism, and more acceptance of modern educational technology being used in big cat enclosures in zoos (Bennett & Johnson, 2021; Cohen, 2019). The Australian public showed higher preferences in environmental conditions for managing big cats in zoos. This may represent greater opportunities for the public to encounter naturalistic exhibits with enrichment items for big cats, and develop deeper understandings about welfare initiatives (Davey, 2007b). In contrast, and perhaps indicating the natural presence of big cats, India showed stronger positive attitudes towards partnering with zoos for CSR projects, undertaking fundraising events and donating to zoos' partnerships in the wild for interacting with the big cat management, thus, highlighting the influence of community outreach programs (Walker, 2012). Neutral views were shared by participants from both countries for feeding of live prey to big cats, having old and injured big cats in zoos and breeding of big cats should only be in a native country for conservation, as viewed similarly in another study by the UK zoo visitors in 1995 (Ings, Waran, & Young, 1997), but somewhat positive views about breeding of big cats only for reintroduction to the wild. The differences in attitudes may also be present due to the differences in overall management of zoo practices amongst Asia-Pacific having an influence on the visitors, as seen in previous research (Teng, 2015).

One of the main reasons for visiting zoos was to spend time with family or friends which varied with the age groups in our study. This reason was more common among older and middle-aged adults, emphasizing the importance of positive family life and the role of zoos in leisure time (Hallman & Benbow, 2007). However, the older aged participants expressed opposing views towards visitors being allowed to walk with big cats, visitors feeding big cats, visitors posing with big cats and their cubs compared to middle-aged individuals which could indicate generational differences and legacy thinking (Gao, Zhang, & Huang, 2018; Kleespies et al., 2021; J. A. Taylor & Duram, 2021). This may also be why middle and younger-age groups were keen to have more enrichment items for big cats, which was similar to younger respondents in previous research (Carnovale et al., 2022), while older aged individuals preferred having social animals to be kept in groups and solitary animals alone. Thus, we found

no consistency among the age groups in their attitudes which aligns with other studies assessing the welfare of animals (Randler, Ballouard, et al., 2021).

Attitudes toward animal welfare usually differ between genders (Herzog, 2007), with higher positive pro-animal attitudes among females than males (Apostol, Rebega, & Miclea, 2013; Herzog et al., 1991; Kellert & Berry, 1987; Martens, Hansart, & Su, 2019; Mazas, Fernández Manzanal, Zarza, & María, 2013; Pagani, Robustelli, & Ascione, 2007). We found similar trends in our research with females showing more consideration towards learning about big cat conservation as a reason for visiting zoos, with being more attracted to unique feline/cat behaviours as the most liked aspects of big cats. Females also strongly agreed that selective breeding of big cats, such as white tigers, may affect big cat conservation negatively but they held somewhat neutral views about seeing injured or old big cats in zoos compared to males highlighting varying levels of empathetic responses as reported in past work (Carnovale et al., 2022). Our results also show that males somewhat more agreed with the view of killing big cats involved in negative incidences, encounters or attacks than females; this may reflect males' interests in hunting, trapping or fishing as wildlife-related recreation (Hendee, 1971; Hobson, 1979; Kellert & Berry, 1987). These gender differences may be due to underlying propositions such as females share more care and nurture due to the egalitarian and social behaviours linked to social identity theory as compared to the less emotional, utilitarian attitudes in males (Herzog et al., 1991; S. Knight, Vrij, Cherryman, & Nunkoosing, 2004; Randler, Ballouard, et al., 2021; Stets & Burke, 2000; W. Wood & Eagly, 2002).

Our hypothesis that education could play a role in shaping the attitudes of the public towards big cats was rejected, as we found no difference across the parameters measured. Other studies also report no correlation between higher education and visits to zoos (Davey, 2007a). Further, in relation to the welfare of other species, such as reptiles, no relationship was found between the respondents' welfare score and their level of education (Devlin & Ogle, 2022). These results suggest that education and other social or demographic factors may work together in influencing attitudes.

However, contrasting results where education plays a role in influencing attitudes have also been reported, with individuals with a higher education level showing more concern for captive animals (Gurusamy et al., 2015; Teng, 2015); a higher education background is also linked to socio-economic status and more interest and affection towards the natural world (Davey, 2006, 2007a; Kellert, 1996).

The number of zoo visits can impact the attitudes of the people to varying degrees (L. Smith, Broad, & Weiler, 2008). Overall, we found the more frequent the number of zoo visits the stronger a relationship with various subscale parameters i.e., frequent zoo visitors were associated with concerns for big cats in zoos and the zoo's welfare practices; this is reported in other research towards zoo animals in general (Davey, 2007b; Devlin & Ogle, 2022; Reade & Waran, 1996). However, these results may not necessarily imply cause and effect, and also contradict the findings of other studies that show no direct relation between the number of zoo visits and concern for animal welfare, and may also be associated with entertainment and tourism (P. Mason, 2000; Ryan & Saward, 2004). Further, as the zoo visits increased, seeing rare and endangered big cats was a primary reason for visiting zoos. This correlates with previous research that being 'endangered' was the most important trait for a zoo animal to attract visitors (Carr, 2016). We also found that the most liked aspects of big cats, specifically colours/ coat patterns, hunting skills, unique feline/ cat behaviours and the whole animal increased strongly as the number of zoo visits increased. Our findings echo a study of the Malaysian population which showed visitors preferred seeing attractive and active animals (Puan & Zakaria, 2007).

For the environmental conditions designed for big cats, we found that with an increase in zoo visits there were higher preferences for the cats' welfare. Factors included enrichment items for big cats, keeping social animals in groups and solitary animals alone, providing good hiding spots for big cats even if viewing is more difficult for visitors, along with enough enclosure space between different cat enclosures and less intrusive ways to observe them. Using safari buses to view big cats and watching live video streaming of big cats were preferred encounters with big cats.

This suggests a wider awareness and acceptance of zoos using innovative technologies to provide virtual experiences to the public. However, more neutral perceptions emerged about visitors being allowed behind the scenes for a closer look at big cats, this was more so among those who visited the zoo often than others who somewhat disagreed. These variations indicate interactive exhibits may provide opportunities for the public to learn more about big cats, as pointed out by Ferguson and Litchfield (2018). Emphasis could be placed on education, especially by keepers who spend a large portion of zoo opening hours in or near an exhibit and interact with the animals as they care for them (Ferguson, 2018). These findings disclose the importance of naturalistic exhibits for visitors who hold a positive perception of these (Godinez & Fernandez, 2019). They also indicate a willingness to opportunistically view animals, which contrasts with results from other countries (Ryan & Saward, 2004). Similar to these findings, a study assessing reptile welfare reported a strong relationship between the number of annual visits and positive perceptions of enclosure size and the physical space afforded to reptiles among more frequent visitors (Devlin & Ogle, 2022). In providing quality naturalistic enclosures for animals, zoos can implicitly and explicitly contribute to conveying positive views about animal welfare and conservation (Puan & Zakaria, 2007).

Our results also suggest that an increase in zoo visits may promote more interest in attending keeper talks, visiting the zoo animal hospital if permitted, participating in research or volunteering opportunities at the zoo, talking to keepers about the well-being of big cats, buying gift certificates to adopt rescued or injured big cats and donating to zoo partners to support big cats in the wild. The increased interest of zoo visitors to participate in these activities and online on-site and off-site conservation activities and efforts resonates with other research findings (Godinez & Fernandez, 2019). Among the shared welfare concerns for big cats such as breeding should only be for the reintroduction to the wild, the number of zoo visits variously influenced attitudes. More positive views were evident among those who visited the zoo least, i.e., less than 5 times. Those who visited over 10 times had stronger views towards boredom affecting big cats, with this group holding more neutral views about killing of big cats involved in negative incidents, encounters, or attacks, and having old or

injured big cats in zoos. These insights show charismatic animals may attract more welfare-related concerns from different visitors as compared to other animals at the zoo (Hosey et al., 2020). Our findings also contrast with other studies that reported no relationship between the number of zoo visits and participants' perceptions of animal welfare (Devlin & Ogle, 2022).

5.5.2. Two-way and three-way interactions affecting attitudes towards big cats and their welfare

The high number of demographic factors assessed in this study and various two-way and three-way interactions also influenced the attitudes of the public towards big cats and their welfare. Among all the two-way interactions, the age of zoo visitors was found to be influential for three constructs. These included first, the most liked aspects of big cats such as hunting skills, unique feline/cat behaviours, cubs; second, environmental conditions for big cats such as preferred hiding spots for big cats to rest and have privacy (which may not be visible to visitors); and third, talking to keepers about the big cats' well-being, undertaking fundraising events for rescued big cats (e.g. bake, art or photograph sale, etc.), donating to zoo partnerships to support big cats in the wild as interactions with big cat management. The introduction of zoo educational programs from the 1970s after initial reports on farm animal welfare may account for the effect of age and zoo visits on attitudes towards big cats (Kleespies et al., 2021; J. A. Taylor & Duram, 2021). Age, gender and educational level are the most commonly identified factors influencing attitudes in general (Birney & Heinrich, 1991); we similarly observed the combined effect of these three factors affecting public attitudes to big cats and their welfare. Specifically, our results show that these three factors can predict attitudes towards encounters with big cats such as visitors being allowed to walk with big cats, visitors posing with big cats or their cubs, selfies with big cats, and also interactions and efforts with big cat management such as buying gift certificates to adopt rescued/injured big cats. The literature shows strong associations among these three factors on the individual attitudes with links to social cognitive factors (Ajzen, 1991; Flower, Burns, Jones, & McBroom, 2021). The other two-way and

three-way interactions we found significant had a smaller effect on individual constructs and our findings confirm earlier studies on location and age (Kellert, 1985b); gender and education (Du, Xiao, & Zhao, 2021; Paul & Podberscek, 2000); gender and zoo visits (Martens et al., 2019); location and zoo visits (Kleespies et al., 2021); and location, education and zoo visits (Vicente-Molina, Fernández-Sáinz, & Izagirre-Olaizola, 2013) which may be specific to attitudes and the populations surveyed.

5.5.3. Limitations and future directions

Several limitations are recognised in this research. As the online surveys were administered using a snowball approach, the overall reach of the survey cannot be measured; although it potentially may have reached wider audiences, people may have opted not to participate. Further, these findings are species and location specific meaning there is potential for a social response bias to exist. This bias may be prevented in upcoming studies if they include items that check for a social response bias. Future avenues of research in this area can include examining other social, cultural and political factors specific to states and regions. At a community level, zoos could seek to proactively evaluate visitors' perspectives about their animals using the practical and established I-Change model. This model, which measured the efficacy of the interactive TigerTrek Exhibit at Taronga Zoo in influencing visitors' tiger conservation attitudes and behaviours (Kelly & Skibins, 2021), can help to educate the general public. Incorporating such models that use modern technology to record and assess demographic factors could help zoos reach wider audiences on a long-term basis.

5.6. Conclusions

This research explores and shows current attitudes of the general public in India and Australia towards the captive management of big cats and their welfare. It further

identifies demographic factors that influence these attitudes. The results show the number of zoo visits is the most significant factor impacting the attitudes of the general public in both countries, with other demographic factors such as location, age, gender and education level influencing some attitudes. This information provides zoos with information to facilitate and target the engagement and efforts of specific audiences, and to advocate for positive human-animal attitudes through welfare initiatives. It also provides zoos with a framework to proactively manage big cats in captivity and promote their welfare.

Acknowledgement

We are extremely grateful to the participants who contributed to this study.

Authors' contributions

JV and JH conceived and designed the study; JV collected data; JV and JH analysed the data and interpreted the results; JV wrote and prepared the manuscript; JV and JH revised the manuscript. The authors read and approved the final manuscript.

Funding

The study was supported by the Research Training Program (RTP) Stipend from Western Sydney University to JV. JH was supported by a grant from the Australian Research Council (DP180101708). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Chapter 6: Stakeholders' perception of human-leopard interactions- A preliminary study of Sanjay Gandhi National Park, Mumbai

6.1. Abstract

Loss of natural habitat and encroachment means there are increasingly more frequent interactions between humans and wild animals, and direct interactions with big cats may impact the lives of people and the animals. More recently, stakeholder involvement in protected areas has the potential to raise awareness and contribute to the ongoing narratives about big cats cohabiting with humans in megacities. Therefore, understanding the perceptions of the key stakeholders is necessary to determine their role in conservation and the future of the parks. However, perceptions may vary due to various factors, and it may get more complex in urban areas with many stakeholder groups having varied interests. Thus, using the case study of Mumbai, this research assesses the current perceptions of thirty-five active stakeholders belonging to seven groups around Sanjay Gandhi National Park (SGNP) towards human-leopard interactions using an online-survey followed by a semi-structed interview. We investigated their a) attitudes towards leopards as an animal and leopards as an issue, b) attitudes about management strategies for leopards, c) perceived threats to Mumbai's leopards, and d) views about factors contributing to reduction in leopard attacks. The findings show that the seven stakeholder groups assessed, have similar perceptions towards leopards as an issue, threats towards the leopards and factors contributing to the reduction in leopard attacks. In landscapes where humans and big cats coexist, there needs to be tolerance and common goals that can safeguard both people and animals, and this case study can be used as a model to identify conservation priorities elsewhere.

Keywords: big cats, human-wildlife interactions, *Panthera pardus fusca*, stakeholder engagement

6.2. Introduction

Globally, humans and carnivores share overlapping spaces and may interact occasionally with each other (N. H. Carter & Linnell, 2016). These human-wildlife interactions may be positive, neutral, or negative depending on the type of interactions (Bhatia, Redpath, Suryawanshi, & Mishra, 2020). For example, human-leopard interactions (HLI), may be positive interactions of coexistence; they may also be adverse and involve conflict with loss of human life, livestock, or property. Early studies on HLI aimed to provide immediate solutions emerging from attacks on people and livestock. These included providing monetary compensation to those who suffered loss and relocating these leopards elsewhere or translocating them to a rescue centre permanently (Athreya, 2006; Athreya, Odden, Linnell, & Karanth, 2011; Ghosal, 2012; Ministry of Environment and Forest, 2011). However, findings show leopards tend to return to their home territory (as reported in a radio-collared leopard named *Ajoba* who travelled 120 km back to his original habitat in 24 days), and translocation to unfamiliar environments may cause stress that can increase attacks on humans by translocated leopards near the release sites (Athreya et al., 2011), impact the wild animal's welfare and coping ability (Vaz et al., 2017), ultimately impeding conservation efforts (Athreya, 2006; M. J. Dickens, Delehanty, & Michael Romero, 2010).

It is well established that human-wildlife impacts are strongly affected by relationships between different groups of people (Redpath et al., 2012). These social aspects are often ignored, even though they affect the issue much more than the ecology of the wild animal. Recent insights of the eight core principles - Presence, Aptness, Respect, Transparency, Negotiation, Empathy, Responsiveness and Strategic Support (PARTNERS) bring to light the role of local communities and stakeholders in human-wildlife interactions (Mishra, 2016). These have been effectively applied on the endangered snow leopard *Panthera uncia* and its mountain ecosystems and communities in South and Central Asia (Mishra, Young, Fiechter, Rutherford, & Redpath, 2017). However, this may not be a straightforward approach as the complexity of urban cities with wildlife and the social disparities in a landscape may

force wildlife to co-exist, but present unique challenges with differing outcomes such as in Nairobi and Mumbai (Landy, Rodary, & Calas, 2018). The 'stakeholder analysis' approach is a recent approach in conservation and can be useful to understand stakeholder's perspectives; their changing perceptions about a topic or the impacts of an issue (Nagulendran et al., 2016). Studies involving local stakeholders have been successful in facilitating serious conservation management to safeguard the welfare of wild felids in various protected areas of South-east Asia (T. D. Allendorf, Smith, & Anderson, 2007; Udaya Sekhar, 2003). Participation and collaboration among different groups or stakeholders provides the platform to develop unique relationships and interactions, to inform the best interests of everyone associated with the animals.

With the improvement in the understandings towards HLI, there has been changes in management strategies such as the formation of specialist groups to create global dialogue and support professionals through interdisciplinary guidance, resources, and capacity building such as the IUCN SSC Human-Wildlife Conflict & Coexistence Specialist Group (formerly IUCN SSC Human-Wildlife Conflict Task Force). In India, people and wildlife have interacted and coexisted since many years and the diverse ethno-sociological traditions may influence their tolerance and perceptions towards leopards throughout India (Ghosal, 2018; Oommen, 2021; Zerah, Tawa Lama, Dupont, & Chaudhuri, 2011). For example, some indigenous locals from human-dominated regions in Western Maharashtra reportedly interact with or live among wild leopards (*Panthera pardus fusca*) and also worship them as *Waghoba*- the leopard deity (Nair et al., 2021). Likewise, the locals of northern India hold various unique beliefs about leopards as thinking beings and protectors (Dhee, Athreya, Linnell, Shivakumar, & Dhiman, 2019). Further, previous studies found that the local population in southern India had neutral to negative feelings towards leopards due to their past experiences (Sidhu, Raghunathan, Mudappa, & Shankar Raman, 2017).

The Sanjay Gandhi National Park has one of the highest density of leopards (*Panthera pardus fusca*) in the world and is located within the city limits of Mumbai. Sharing spaces with leopards in urban landscapes comes with its own complexities and requires unique efforts to protect both the animals and people (Treves & Karanth, 2003). Before 2005, and coinciding with the highest relocations of leopards, there were

many attacks. Post 2011, there has been a decline in attacks after guidelines for managing HLI were implemented and the Forest department began collaborating with various stakeholders and organising leopard awareness workshops (Bhatia, Athreya, Grenyer, & Macdonald, 2013; Ministry of Environment and Forest, 2011). In 2011, the Forest department initiated a project called *Mumbaikars for SGNP* (MfSGNP) to conduct research into leopard ecology, understand HLI, and engage in dialogue with various stakeholders to facilitate human-leopard coexistence in and around Mumbai (Ghosal, 2018).

Between 2011 – 2014, studies in SGNP reported various perceptions of HLI from the perspectives of media (Hathaway et al., 2017), forest department officials (Ghosal, 2018) and both indigenous and non-indigenous locals (Athreya et al., 2018; Edelblutte & Gunnell, 2014; Ghosal, 2018). The indigenous communities living inside SGNP, and their lifestyle and religious beliefs, are more nuanced allowing for complex interactions between them and the resident leopards (Nair et al., 2021). Fellow Mumbaikars living around the park who occasionally spotted leopards had a different view (Landy, Rademacher, & Sivaramakrishnan, 2017; Nair et al., 2021; Rose, 2021). These varying perceptions may be based on knowledge, personal experiences, values, cultures, beliefs, social media, and wider societal experiences (Estep & Hetts, 1992; Landy et al., 2017; Te Velde et al., 2002; Zulkifli, 2013).

Perceptions can also vary depending on priorities. Disagreements between stakeholders may arise due to their own interests such as park conservationists working for animals versus locals who may fear for their safety. Such divergent perspectives can be a challenge to manage and determine preferences for incidents. However, this may also provide opportunities to identify differences (pluralism) and collaboratively work towards addressing them (De Lopez, 2001; Jhamvar-Shingote & Schuett, 2013). As HLI is a phenomenon that will continue, it is important to understand perceptions toward leopards and identify preferred mitigation strategies to inform the future of HLI (Sen & Nagendra, 2019). Assessing the role of an individual stakeholder may also help in shifting perceptions, prompt like-thinking and contribute to working toward and achieving the same goals of HLI (Sutherland &

Woodroof, 2009; Varma et al., 2015). Therefore, multi-stakeholder participation is important in identifying priorities during HLI, promoting inclusiveness in the community and in helping to reduce bias while developing agreeable strategies and taking ownership of wildlife interactions and issues.

This study assesses the current perceptions of stakeholders around SGNP in Mumbai towards HLI to contribute to the ongoing narratives about leopards cohabiting with humans in megacities. It focuses specifically on reviewing significant events of HLI in the park in the last few years since changes were implemented by the forest department. The study also assesses stakeholders' a) attitudes towards leopards as an animal and as leopards as an issue (those that share the same space), b) attitudes about management strategies for leopards, c) perceived threats to Mumbai's leopards, and d) views about factors contributing to reducing leopard attacks. We aim to identify the stakeholders and determine similarities and differences in stakeholders' perceptions and if the role of the stakeholder influences their perceptions. We hypothesise that due to the interconnectedness of stakeholder groups and involvement in the park, there may be fewer differences in perceptions. Further, additional information on the sources of their current knowledge, involvement/interactions with other stakeholders and their role in HLI were also gathered to gain insights into the factors underlying their perceptions. Thus, this study aims to identify the strategies that are socio-culturally acceptable to the different stakeholders in the SGNP area. It also aims to inform an up-to-date positive outcome for co-existence and conservation to improve HLI, in SGNP thereby enhancing the welfare of the wild leopards.

6.3. Material and methods

6.3.1. Study area

In the western region of India, within the state of Maharashtra lies the Sanjay Gandhi National Park; a 103.84 sq. km. protected forest area that is surrounded by the city of

Mumbai (19° 8' N, 72° 53' E and 19° 21' N, 72° 58' E) (Figure 6.1). This national park supports a rich biodiversity of flora and fauna, including carnivores such as leopards (Edgaonkar & Chellam, 1998; Surve, 2015; Yazdani, Pradhan, & Singh, 1992). Recently, in 2020, an additional area of 812 acres from the Aarey Colony in the south has been added to the SGNP as an eco-sensitive zone. This was a result of the constant efforts of *Mumbaikars* fighting to protect this area as it had frequent leopard sightings, biodiversity, and indigenous land significance. The park is managed by the SGNP Forest Department, and according to their latest mammal survey 47 leopards were recorded living inside SGNP in 2019, without any fatal leopard encounters since 2018 (Ghai, 2019). Leopards are listed in the Schedule I category of the Indian Wildlife (Protection) Act, 1972 and are also included in Appendix I of CITES (Discover CITES, 2008; The Wildlife (Protection) Act, 1972). As per the IUCN RedList, they are listed as Vulnerable (Stein et al., 2016).

For the last 2000 years or more, humans have been connected with SGNP, as evidenced by the Buddhist archaeological remains called the *Kanheri* caves inside the park (Negi, 2002; Zérah, 2007). SGNP is currently home to indigenous *Adivasis* such as the *Warli,* the *Mahadeo Koli,* the *Malhar Kolis,* the *Kokna,* the *Dubla,* the *Katkari and* the *Thakker/Thakur* who live in small hamlets called '*padas*' inside the park, along with some non-indigenous inhabitants (Edelblutte & Gunnell, 2014; Nair et al., 2021). Some of the indigenous tribes worship the leopards as *Waghoba;* the leopard deity, and *Waghoba* shrines may be seen across the landscape (Athreya et al., 2018; Nair et al., 2021).

As Mumbai's population is growing from 12.47 million in the 2011 census to an estimate of 27 million by 2025, SGNP has become surrounded by residential and commercial areas (Rahaman, Jahangir, Haque, Chen, & Kumar, 2021; Zérah, 2007). The lakes located inside the park provide drinking water to the city of Mumbai (Sen & Pattanaik, 2016), and some areas of the park are frequently used for morning walks, biking, bird watching and there are numerous nature trails and other recreational activities such as visiting the caves, boating, and animal safaris. A secondary review analysis, conducted to understand the significant events occurring in the park,

indicates there have been constant human interactions with the park over the years (Table S6.1). These events, alongside past literature, informed the design of the questionnaire used in the survey and guided the semi-structured interviews.

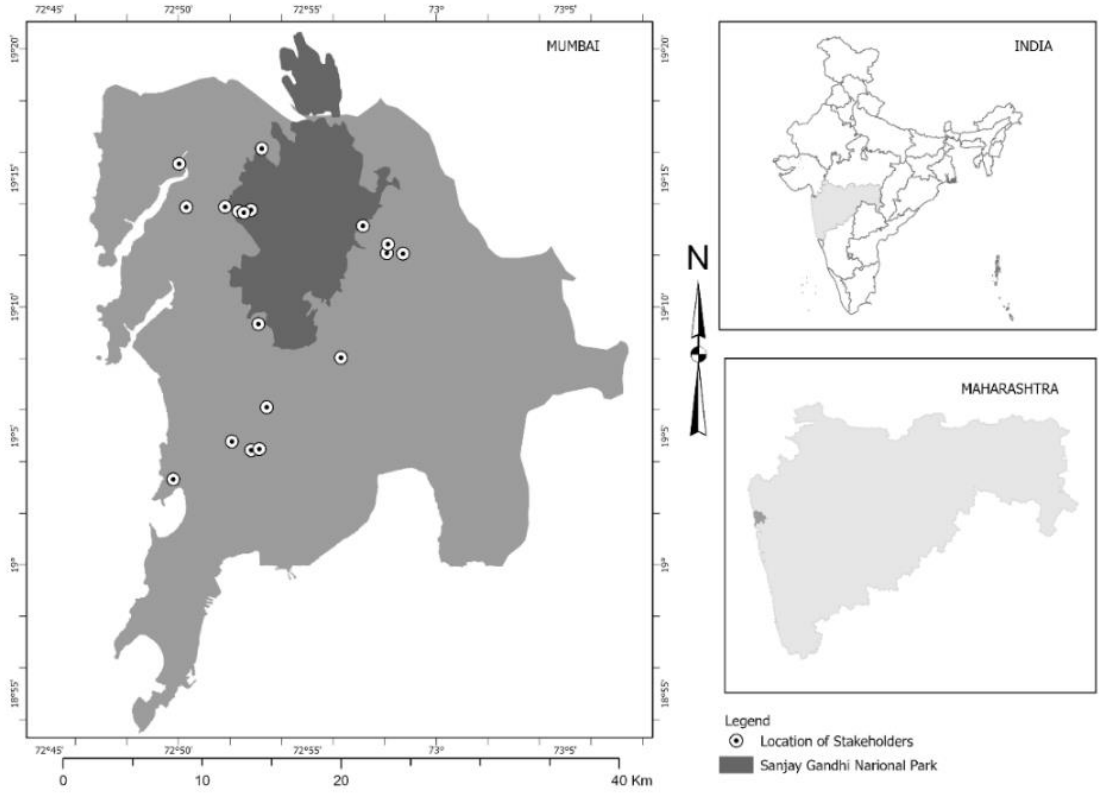

Figure 6. 1 Location of respondents for ethnographic study around Sanjay Gandhi National Park, Mumbai

6.3.2. Survey and interview design

The study was conducted between December 2020 and August 2021 with the approval of the Human Ethics Committee at Western Sydney University (H13741). Based on the 'focal approach' of consulting the key stakeholders of SGNP who had prior experience working in the park, a list of the stakeholder groups was identified (R. O. Mason & Mitroff, 1981; Rastogi, Badola, Hussain, & Hickey, 2010). These stakeholders were classified as i) *local inhabitants* (both indigenous and non-indigenous from SGNP, Aarey and Yeoor), ii) *forest department officials* (Mumbai and Thane Division), iii) *researchers*, iv) *local Non-Governmental Organisations (NGOs)* (Resqink Association for

Wildlife Welfare (RAWW), the World Wide Fund for Nature (WWF), Vanashakti, Bombay Natural History Society (BNHS), GreenLine), v) *civil society groups* (CSGs) (Mumbaikars for SGNP (MfSGNP), Aarey Conservation group (ACG), Urban Biodiversity Conservation group (UBCG), Morning walkers group, vi) *media professionals* (Midday, Hindustan Times, Times of India, DNA/Mumbai Mirror, Sakal Media), and vii) *university student volunteers* (Wilson College, K J Somaiya College of Science & Commerce, St Xavier's College, VIVA College, Bhavans College) (Figure 6.2). To decrease the potential bias associated with having a higher number of stakeholders in any particular group, a total of 35 participants were recruited with a limit of five respondents per stakeholder group (Guest, 2015; Lewis, 1996). The selection of the participants for this study was purely based on their role and involvement in the park, irrespective if they attended any workshops held by the Forest Department.

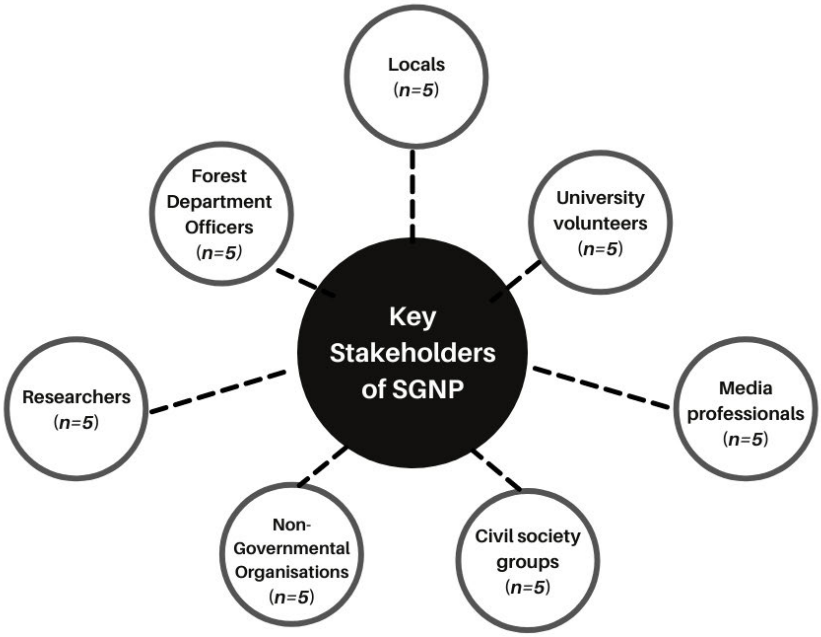

Figure 6. 2 Targeted stakeholder groups of Sanjay Gandhi National Park (SGNP) interviewed for the study (n= 35)

The local inhabitants belong to a mixed population of ethnic groups living together and can be classified as indigenous tribals and domestic migrants belonging to different economic groups of the Indian society (Surve, 2015). The tribal inhabitants may depend on the forest for firewood, while the lower and upper-class migrant residents travel outside the park to earn daily wages. The tribal inhabitants living near, or inside the forest, may fear and respect the leopard deity as *Waghoba* with small shrines across the region where people worship *Waghoba* seeking protection (Athreya et al., 2018). The SGNP forest department comprises of permanent forest staff members working at the park. The park's jurisdiction is spread across two territorial divisions that lie in the district of – Mumbai and Thane. The officers are of different ranks, and they perform different duties in the department. SGNP is an important location for researchers to study wildlife and numerous studies have occurred in and around the park (Ghosal, 2012, 2018; Surve, 2015). Alongside these stakeholders, local NGOs work around the park, assisting with the handling of any wildlife situation, and spreading awareness about the wildlife among the wider population of city dwellers. The civil society groups consist of individuals who may or may not live in the immediate premises of the park but are interested in advocating for animal welfare, biodiversity conservation, ecological benefits or human safety in the park. The media professionals play a huge role in publishing stories about the wildlife of Mumbai in various newspapers which can be both positive and negative consequences for the park and its human and wildlife inhabitants. The university students who volunteer for various research projects in SGNP are key to the continued functioning of the park and often advocate for wildlife or social issues in the park and wider Indian society.

The study protocol was conducted in two steps: stakeholders were first invited to participate in an online questionnaire which was followed by an online or face-to-face semi-structured interview. Following Dillman's four-step survey design method, participants were initially approached with a pre-notice letter. They then received a survey link, a reminder message and a follow-up email with the survey-interview details (Dillman, 2000; Dillman, Smyth, & Christian, 2014). Informed consent was obtained from all participants before conducting the study and permission was

received to record the participants' questionnaire and interview responses. Participants could select to participate either online or face-to-face, as dictated by COVID-19 safety requirements. The survey was executed in either English or Marathi language according to the participant's preference. The researcher maintained a field diary for detailed notetaking. All personal information for the participants was de-identified to ensure anonymity and the data were translated and then transcribed into English by the researcher.

6.3.3. Survey items

Mixed methods were used to collect the data. Quantitative data were sourced through close-ended questions in the questionnaire and the short in-depth, open-ended questions in the interview provided the qualitative data (Gay, Mills, & Airasian, 2009). A questionnaire with preliminary questions were pilot tested with a small group of researchers and locals. These responses informed refinements to the data collection tools to include terminology familiar to the stakeholders and to reduce bias (Schuman, 1986). The revised questionnaire consisted of ten sections and was designed on Qualtrics web-based software (Qualtrics LLC, Provo, Utah, USA) (Figure S6.1). The first section collected data on the respondent's background such as location, age, gender, education level, occupation, and stakeholder role. The next section was aimed at assessing the stakeholder's a) attitudes toward leopard as an animal and as an issue, b) attitudes about management strategies for leopards – when should a leopard be captured or kept permanently in captivity, c) perceived threats to Mumbai's leopards, and d) perceived factors contributing to the reduction in leopard attacks.

These perceptions were measured by using a series of statements, which were rated on a 5-point Likert scale (1: Strongly disagree, 2: Somewhat disagree, 3: Neither agree nor disagree, 4: Somewhat agree, 5: Strongly agree). A Likert scale is commonly used in human-wildlife interaction research to measure the attitudes of people according to their level of tolerance (Likert, 1932; Whitehouse-Tedd, Abell, & Dunn, 2021). The last set of questions in the questionnaire collected information on the

sources of stakeholders' current knowledge and their involvement/interactions with other stakeholders based on a series of multiple-choice questions.

On completing the questionnaire, participants were asked four open-ended questions during an individual follow-up interview. The interview questions gathered information on the stakeholder's organisation and role, their mode of communication, challenges faced and possible influences on HLI in Mumbai. The interviews were conducted via Zoom (Zoom Video Communications, Inc., USA, version 5.7.7) or face-to-face at a place convenient to the respondent. It was reiterated that their responses were to be focused on SGNP and its leopards only. On average, interviews lasted for about 20 – 30 mins.

6.3.4. Preliminary graphs

The Likert scale responses from the questionnaire were represented in the form of a diverging stacked bar chart in RStudio version 1.2.5033 (RStudio, Inc. Boston, MA). The stacked bar chart explicitly shows the variation across the multi-scale items among the individual responses (Figures S6.2-S6.7). The sources of stakeholders' current knowledge and their involvement/interactions with other stakeholders was also presented (Figures S6.8). Before conducting any reliability or analyses on a group of items, it is essential to ensure that all items are consistent with each other in terms of what an agreement or disagreement means for the construct/question being measured (Koo & Li, 2016; Revicki, 2014; Shrout & Fleiss, 1979). To achieve this, we reverse scored the items which were negatively phrased by transforming and re-coding the responses in SPSS. This transformed a high score into a corresponding low score on the scale which makes all items consistent. These reverse-scored items were then used for all further analysis.

6.3.5. Internal consistency reliability

The construct of interest was rated on a Likert scale; this is a multi-item measurement scale with a set of *k* items whose reliability needs to be considered (Coolican, 2014; Langdridge & Hagger-Johnson, 2013; Revicki, 2014). To test the internal consistency reliability, we used the Cronbach's alpha (α) reliability coefficient for the six constructs (Cronbach, 1951; Tavakol & Dennick, 2011). The α coefficient value ranges between 0-1, where values closer to one indicate higher reliability and greater consistency of the items contained within the scale. Nunally (1978) recommends a minimum α level of 0.70 to be highly reliable. However, α is dependent on the number of items in the scale and a smaller number of items in a scale (fewer than 10) can lead to a lower α. Since our scale had smaller scale items, the α values could be low for this reason (Table 6.1). Due to the sensitive nature of α, it is recommended to conduct more than one reliability measure and a substitute for the α is the McDonald's omega (ω), which is a more general estimator and more suitable for applied research (Deng & Chan, 2017; Dunn, Baguley, & Brunsden, 2014; Hayes & Coutts, 2020).

The McDonald's omega (ω) was installed as a macro in the SPSS software following the steps and code generated by Hayes and Coutts (2020). The ω does not assume essential tau-equivalence yet reduces to α under the assumption of essential tau-equivalence (Hayes & Coutts, 2020; R.P. McDonald, 1999). Thus, reliability scores obtained through the ω coefficient can overcome some limitations present in α, such as being affected by the number of items or working with continuous variables, which may not occur in social sciences (Jöreskog, 1971; R. P. McDonald, 1970; R.P. McDonald, 1999). Similar to α values, although there is no strict rule of thumb, the ω value of 0.7 and above are generally considered highly reliable, with 0.6 - 0.7 as moderately reliable, while 0.5 - 0.6 may be acceptable measures and relies on professional judgement (Crutzen & Peters, 2017; Ursachi et al., 2015). We found one construct (Q5) had highly reliable ω values. Further, on reducing the subscales for the other constructs by the "leave-one-out" method in SPSS (Hayes & Coutts, 2020), Q1, Q2, Q4, and Q6 had moderate and acceptable reliability. Depending on the field of research, lower reliability scores may also be used with caution (Lance, Butts, & Michels, 2006).

The remaining construct (Q3) with lower values was removed from further analysis because the scores did not pass the reliability test and could contain random measurement errors.

Table 6. 1 Reliability measure using Cronbach's alpha (α) and McDonald's omega (ω)

Construct questions	**α**	**ω**	**ω (leave-one-out method)**
Q1 - Perception of leopards as an animal	-0.316	0.054	0.521 (with 1.2, *R*1.3, 1.4, 1.5)
Q2 - Perception of leopards as an issue	0.115	0.348	0.660 (with 2.1,2.3, 2.5,2.6)
Q3 - When should a leopard be captured?	0.290* (without Q3.2)	0.353* (without Q3.2)	-
Q4 - When should a leopard be kept in captivity permanently?	-0.564*	0.002 (without Q4.1)	0.529 (with Q4.2, Q4.3, Q4.4)
Q5 - Threats to urban leopards in Mumbai	0.707	0.728 (with all)	
Q6 - Factors contributing to the reduction of leopard attacks in Mumbai?	0.773	0.789 (with 6.1, *R*6.2, 6.3,6.4,6.5)	

(*items with full agreement automatically removed from analysis), (*R*= reverse-scored data)

6.3.6. Data analysis

The socio-demographic data were analysed using descriptive statistics in IBM SPSS version 27.0 (SPSS Inc., Armonk, NY, USA) to describe the background of the respondents. Next, a multivariate analysis of variance (MANOVA) and a one-way ANOVA was calculated on the reliable sub-scale scores to measure similarities and differences in the stakeholders' perceptions.

Discriminant Function Analysis (DFA) was also conducted. Discriminant Function Analysis can classify respondents into groups by assessing the extent to which independent variables successfully classify the dependent variable and by determining the extent to which the independent variables explain the variance in the dependent variable (Fisher, 1936; Stevens, 2002). In this study, DFA was used to predict stakeholders' roles (i.e., locals, forest department officials, researchers, NGO members, CSG members, media professionals and volunteers) from a linear combination of multiple dependent variables that passed the reliability test (i.e., perception of leopards as an animal and as an issue, perceived threats to urban leopards and perceived factors leading to a reduction in leopard attacks) (Wald, Jacobson, & Levy, 2013). Further, DFA creates functions to indicate whether these significantly discriminate between groups. This process uses a combination of dependent variables and provides estimates of % variance, canonical R^2, and significance (Wilks Λ and χ^2), and also provides a classification table showing whether individuals were correctly classified into groups. Variables above 25% are generally accepted (Burns & Burns, 2008). The qualitative data were collated to describe the role of the stakeholder, the nature and level of their activities, and possible influences on HLI.

6.4. Results

6.4.1. Socio-demographic characteristics of SGNP stakeholders and their role

Of the 37 participants approached, 35 willingly agreed to participate in the study. The study collected the following demographic variables. Of the 35 stakeholder participants, 27 were male (77.1%) and 8 were female (22.9%). Twelve participants (34.3%) were in the 18-28 years group, 9 (25.7%) were 29-38 years, 8 (22.9%) were 39-48 years, 5 (14.3%) were 49-58 years and 1 participant (2.9%) was 58+ years. The educational qualifications showed that 2 participants (5.7%) had completed Primary - Secondary school, 1 (2.9%) had completed Secondary school – College, 8 (22.9%) had

completed College - Undergraduate degree, 2 (5.7%) had completed a Diploma, and 22 (62.9%) had completed a Higher postgraduate degree.

The qualitative data describing the stakeholder's role and possible influences on HLI are described in Table S6.2.

6.4.2. Stakeholder perceptions towards the SGNP leopards using MANOVA and ANOVA

Although stakeholders' perceptions towards leopards as an issue varied, it was not significant among the different stakeholder groups, as the MANOVA demonstrates. There was no significant difference in the perceived threats for leopards among the different groups of stakeholders. Similarly, there was no significant difference in the perception of factors contributing to a reduction in leopard attacks between the stakeholders (Table 6.2).

A univariate ANOVA further showed a similarity in perceptions except for Q5.3 which showed a significant difference in stakeholders' perceptions of Poaching as a threat to leopards. However, this may be due to chance, or the number of variables used (Table 6.2).

Table 6. 2 Multivariate analysis of variance (MANOVA) examining the effects of stakeholder's role on the perceptions of leopards in SGNP, Mumbai

MANOVA				
Model terms	**Pillai's Trace**	**df**	***F***	***P***
Q2. Perception of leopards as an issue	0.774	6, 28	1.119	0.336
Univariate ANOVAs				
Model terms	**(Perceptions)**	**df**	***F***	***P***
Stakeholder's role	Q2.1- Just like humans, leopards are adaptable & found in most parts of India	6, 28	0.922	0.494
	Q2.3- Leopard numbers depend on the availability of food like deer, pigs, dogs	6, 28	0.965	0.466
	Q2.5- Leopards can share space with humans peacefully	6, 28	1.452	0.231
	Q2.6- If our surroundings clean and litter free, we will not have much of leopard presence	6, 28	0.702	0.65
MANOVA				
Model terms	**Pillai's Trace**	**df**	***F***	***P***
Q5. Threats to urban leopards	1.456	6, 28	0.890	0.683
Univariate ANOVAs				
Model terms	**(Perceptions)**	**df**	***F***	***P***
Stakeholder's role	Q5.1- Linear infrastructure	6, 28	0.182	0.98
	Q5.2- Road kills	6, 28	0.397	0.875
	Q5.3- Poaching	6, 28	2.79	**0.03**
	Q5.4- Decline in prey	6, 28	2.108	0.084
	Q5.5- Dumping of debris	6, 28	1.268	0.304
	Q5.6- Illegal liquor dens	6, 28	0.855	0.539
	Q5.7- People's intolerance to wild animals	6, 28	1.003	0.443
	Q5.8- Bad bureaucratic management	6, 28	0.529	0.781
	Q5.9- Negative reporting by media	6, 28	0.33	0.915
MANOVA				
Model terms	**Pillai's Trace**	**df**	***F***	***P***
Q6. Factors contributing to reduction of leopard attacks	0.693	6, 28	0.751	0.818
Univariate ANOVAs				
Model terms	**(Perceptions)**	**df**	***F***	***P***
Stakeholder's role	Q6.1- Awareness about facts & cautious leopard safety practices	6, 28	1.625	0.177
	QT6.2- There are very few leopards left now in SGNP	6, 28	1.139	0.366
	Q6.3- Formation and active participation of citizen science groups	6, 28	0.914	0.5
	Q6.4- Accurate Media representation	6, 28	1.065	0.406
	Q6.5- Prompt action from Forest Department and other authorities such as police, BMC	6, 28	2.126	0.082

Boldface indicates significance

6.4.3. Identifying the role of the stakeholder as a predictor of stakeholder perception

Firstly, we ran the DFA using the acceptable, moderate, and highly reliable scales (Q1, 2, 4, 5, 6) (Table S6.3). However, as the structure matrix function values were low, we used only the moderate and highly reliable scales for further analysis (Q2, 5, 6) as they explained the functions better. From the reliably rated scale items (Q2, Q5 and Q6), we conducted a DFA on the seven stakeholder groups to predict if their perceptions were based on their role. The results generated six functions, of which three contributed to maximum loadings. Function 1 explained 51.9% of the variance with canonical $R^2 = 0.916$, and function 2 explained 19.1% of the variance with canonical $R^2 = 0.810$. The full model (functions 1 through 6) discriminated between the stakeholder groups Wilks' $\Lambda = 0.008$, $\chi^2_{(108)} = 104.909$, $P = 0.566$, but it was not significant. The second function showed Wilks' $\Lambda = 0.047$, $\chi^2_{(85)} = 65.687$, $P = 0.940$ after removing the first function. Thus, the model classified 91.4% of the stakeholder groups correctly.

Negative and positive perceptions loaded on the three functions, but in opposite directions. Factor loadings indicated negative responses to 'Poaching' contributed strongly to function 1. Positive responses to the 'Awareness about facts & cautious leopard safety practices,' 'Leopards can share space with humans peacefully' and 'There are very few leopards left now in SGNP' contributed to Function 2. Negative responses to 'Prompt action from Forest Department and other authorities such as police, BMC' contributed to Function 3. Across Functions 1, 2 and 3 there was no significant discrimination between stakeholders' perceptions (Table 6.3).

Table 6. 3 Summary of the discriminant functions obtained from the discriminant function analysis (DFA) with reverse-scored acceptable, moderate, and high-reliability subscales for Q2, Q5 and Q6. The analysis yielded three functions with eigenvalues >1 that explained 88.1% of the total variation for predicting group membership. Wilks' lambda revealed no significance in the discriminant function. This model classified 82.9% of the original grouped cases, and 17.1% of cross-validated grouped cases correctly.

Dependent variables	Function		
	1	2	3
Eigenvalue	5.198	1.913	1.706
% Variation	51.9	19.1	17.0
Q5.3 – Poaching	**-0.327***	-0.101	-0.031
Q6.3 - Formation and active participation of citizen science groups	0.084	0.254*	-0.078
Q6.5 - Prompt action from Forest Department and other authorities such as police, BMC	0.194	0.135	**-0.329***
Q5.6 - Illegal liquor dens	-0.081	-0.117	-0.250*
Q6.4 - Accurate Media representation	0.107	0.193	-0.236*
Q5.7 - People's intolerance of wild animals	0.150	-0.062	-0.068
Q5.5 - Dumping of debris	-0.028	-0.249	0.213
Q5.1 - Linear infrastructure	-0.065	-0.026	0.009
Q6.1 - Awareness of facts & cautious leopard safety practices	0.111	**0.289**	-0.187
Q5.8 - Bad bureaucratic management	-0.035	0.051	0.159
Q2.5 - Leopards can share space with humans peacefully	-0.029	**0.306**	0.204
Q5.9 - Negative reporting by media	0.058	-0.011	0.110
Q5.4 - Decline in prey	-0.206	-0.195	0.250
Q2.3 - Leopard numbers depend on the availability of food like deer, pigs, dogs	0.122	-0.076	-0.216
Q2.1 - Just like humans, leopards are adaptable & found in most parts of India	0.104	-0.201	0.078
QT6.2 - There are very few leopards left now in SGNP	0.046	**0.283**	-0.106
Q2.6 - If our surroundings are clean and litter-free, we will not have much of a leopard presence	0.111	0.040	0.125
Q5.2 - Road kills	0.034	-0.026	0.150

Discrimination function loadings >0.280, in boldface, show pooled within-groups correlations between discriminating variables and standardized canonical discriminant functions. Variables are ordered by the absolute size of correlation within the function. The asterisk (*) indicates the largest absolute correlation between each variable and any discriminant function.

The results show no difference between the stakeholder groups as they have similar perceptions. Although the DFA showed a variation of 88.1% in the three functions,

there were no discernible or significant differences between the stakeholder groups, which indicates they hold similar perceptions overall. Thus, the results of DFA are largely consistent with MANOVA indicating hardly any difference between the stakeholder groups in their perceptions.

6.5. Discussion

The current study conducted a review analysis of human-leopard interactions in SGNP, Mumbai and identified current stakeholders' perceptions of these interactions. Overall, the results illustrate the value of similar multi-stakeholder perceptions towards understanding leopards as an issue, threats towards leopards in SGNP as part of the urban landscape of Mumbai and factors resulting in the reduction of leopard attacks. The research hypothesis that due to the interconnectedness of stakeholder groups and involvement in the park, there would be fewer differences in perceptions was supported. In addition, the previous leopard awareness workshops held by the Forest Department could have contributed to this (Ghosal, 2018). Having similar perceptions can help to reframe HLIs by creating an opportunity to share and apply lessons across different stakeholder groups.

6.5.1. Role of the stakeholder in human-leopard interactions (HLI)

The literature suggests that multi-stakeholder participation enhances the quality of environmental decisions which may improve HLIs (Brody, 2003; Reed, 2008). SGNP and its unique stakeholders have their own interests and unique interactions and relationships with the park and its leopards, which determines their perception and inter-group interactions. Past studies demonstrate various factors may influence an individual's attitude and beliefs such as the demography, experiential and knowledge factors and culture, the assumed dividing factor such as the role among stakeholders of SGNP was not supported by our findings. Although there are various stakeholder groups involved in a small landscape like SGNP, this study shows three constructs

measuring HLIs that were the most reliable and attracted a wide societal interest. The questions were ranked under various themes which would prompt decision-makers and other stakeholders to make choices.

6.5.1.1. Perceptions towards leopards as an issue

HLI's can represent a major challenge for leopard management if the ecology and habits of leopards are poorly understood. However, as we investigated further the perceptions towards leopards as an issue, the stakeholders shared a common understanding that just like humans, leopards are adaptable and are found in most parts of India, which indicates the adaptability and similar movement patterns of leopards as evidenced across India (Odden, Athreya, Rattan, & Linnell, 2014). Secondly, the stakeholders believed that leopard numbers depend on the availability of food like deer, pigs, dogs, and the diet of the leopards has been documented earlier to show that the human-dominated landscapes generally have a high density of domestic animals which may act as a source of food for carnivores (Robinson et al., 2014; Surve, 2015). In addition, leopards can share space with humans peacefully was agreed by the stakeholders, which also highlights that Mumbai has not had recent fatal leopard attacks (Nair et al., 2021). Lastly, the perceptions that when surroundings are clean and litter free, there will not be much of leopard presence draws attention to the waste disposal problems around SGNP as a major concern (Landy et al., 2017) and that limiting access to food sources with public awareness may be effective in reducing attacks, which has also been beneficial to reduce negative human-bear interactions in other areas (Skrbinšek & Krofel, 2015). Overall, having similar thoughts reduce the fear and portrayal of leopards as problem animals and show tolerance and co-existence.

6.5.1.2. Perceptions of threats towards leopards in SGNP as part of the urban landscape of Mumbai

In the past, SGNP and its leopards have encountered many challenges and in response to the threats perceived for the leopards of Mumbai, there were no differences among the stakeholder groups suggesting that a common concern was held for the future of the leopards and the park. Across the nine questions measured, most of the stakeholders agreed to linear infrastructure, road kills, poaching, dumping of debris, illegal liquor dens, people's intolerance to wild animals, bad bureaucratic management, negative reporting by media, but disagreed that decline in prey were threats to leopards. While there were small individual differences in the views, however overall, they did not differ statistically according to the stakeholder's role. Similar studies in other landscapes were able to identify the threats for the protected areas based on stakeholder interests (Rastogi et al., 2010).

One of the most common issues surrounding urbanisation and land rights, is the belief that linear infrastructure could be threat to leopards, which is valid as there have been tremendous changes around SGNP, impacting not just the park and conservation efforts, but also the lives of the locals (Joshi, 2013). For example, the encroaching development of the metropolitan area in the Aarey colony has been threatening the cultural and environmental priorities of SGNP (Rose, 2021). The other concern raised for the welfare of the leopards was road kills due to competing priorities of transport and development with crowded roads passing through the eco-sensitive zones of the forest (Joshi, 2013). Further, the occurrence of poaching, dumping of debris and illegal liquor dens was also believed to threaten the welfare of leopards, because until date only preliminary data is available about their impacts on SGNP's leopards through rescued operations (Landy et al., 2017; Sharma & Sinha, 2022). In the past, sightings of leopards would create fear among nearby residents who would then pressurize the Forest Department to trap them, suggesting people's intolerance to wild animals, which has also been seen in other regions of negative leopard interactions (Pimpale, 2015). Another threat assumed by the stakeholders was bad bureaucratic management due to the complexities of the politics and policies of

large carnivore management, , for example the threatened eco-sensitive zone - Aarey Colony in SGNP, which is also similarly observed in other regions and countries (Barua, Bhagwat, & Jadhav, 2013; Mathur, 2014). Lastly, the negative reporting by the media was anticipated to be a threat due to the sensational news reporting in the past with less evidence of factual data causing fear among the general public (Bhatia et al., 2013; Hathaway et al., 2017). However, the stakeholders had mixed perceptions and did not believe that decline in prey was a threat to the leopards, which reflects the previous research studies on prey variety and abundance for SGNP leopards (Surve, 2015). Thus, by identifying these common themes across the stakeholder groups, this provides a forum for stakeholders to discuss how best to voice their support and execute specific activities.

6.5.1.3. Perceptions towards factors resulting in the reduction of leopard attacks

Finally, there was no difference in the perceptions towards factors reducing the leopard attacks, which indicates that there has been a proactive response in past incidences, which is also understood by the stakeholders. The stakeholders positively agreed that awareness about facts and cautious leopard safety practices, formation and active participation of citizen science groups, accurate media representation, prompt action from Forest Department and other authorities such as police, BMC were factors contributing to reduction, but mostly disagreed that there are very few leopards left now in SGNP.

With several projects in the park and the active participation of citizen science groups, NGOs and other stakeholders in collaboration with researchers, forest department has helped in raising awareness about facts & cautious leopard safety practices around SGNP (Ghosal, 2012; Nair et al., 2021). Since HLI in SGNP has been ongoing for many years, as highlighted in our review analysis, the implementation of protocols and initiatives by the Forest department such as MfSGNP has led to the active involvement of various stakeholders in the park (Athreya, Thankur, Chaudhuri, & Belsare, 2007). Various training and capacity building programs have been held,

which has got more stakeholders involved through community-based conservation, and has also been applied to other big cats conservation programs in the Indian landscape (Mishra et al., 2017). With these collaborative efforts, there is now more emphasis on prevention strategies and factual representation of HLI in the media (Bhatia et al., 2013; Hathaway et al., 2017) which has improved people's knowledge to coexist with wild leopards in Mumbai (Ghosal, 2012; Ghosalkar, 2018). These outcomes reflect the recommendations in other human-animal interactions where the mitigation strategies suggested are participatory, multi-stakeholder processes that concentrate on building trust and dialogue, with handing over more decision-making power to local groups, and these also reflect the effective role of PARTNERS principles in human-leopard interactions (Mishra, 2016; Nyhus, 2016). The close working relationships across the stakeholder groups and tremendous efforts taken by each stakeholder group, especially on HLIs with keeping up to date with the changes occurring in the park, actively contribute towards informing and sustaining the groups' similar conservation efforts.

6.5.2. Limitations and future directions

While this study brought together a wide range of individuals and organisations, its limitations are recognised. Several other relevant stakeholders such as the Police, Municipality/ City council and Fire department officials were not surveyed in this study due to logistical constraints and COVID-19 restrictions. Their perceptions may likely differ from the other groups involved. Although the study aimed to have equal gender representation, the positions filled by different stakeholders included a much higher representation of men which suggests the small sample size limited to SGNP stakeholders and/or the cultural influences of the study location. A further limitation is that the planned objectives were not as distinct from each other as expected. For example, Q3 and Q4 assessing the management strategies preferred for leopards (When should a leopard be captured and when should it be kept in captivity permanently), had some potential overlap of ideas, making it difficult to classify them. These limitations may have influenced the results and we further recommend that

studies can assess the differences in perceptions of stakeholders that may be influenced by attending previously held workshops by the Forest Department versus those that did not.

Our discussions with the stakeholder groups indicate several areas to develop and enhance the current situation and practices. We advocate appropriately using multilingual modes of communication to reach larger audiences in Mumbai as a priority to garner wider interest and support in actively protecting SGNP. We also advocate developing a legal policy that safeguards SGNP from future developmental projects. Linking the policies of the park with the Aichi Biodiversity Targets such as Strategic Goal E: Enhance implementation through participatory planning, knowledge management and capacity building will further strengthen the commitment of SGNPs' stakeholders to protecting the park and its inhabitants, both indigenous and wild animals. The Aichi Biodiversity Targets were proposed by national governments through the United Nations Convention on Biological Diversity and would be beneficial in further enhancing the relationships and activities between the different stakeholders. Similarly, their relevance also applies by implementing the PARTNERS principles to improve human-animal relationships through community participation, which could be a great model for SGNP stakeholders to work together. These partnerships may help in applying traditional knowledge aimed at protecting the forest and achieving wider social and environmental outcomes, keeping the encroachers away. We also recommend conducting a stakeholder analysis after any new management interventions or policy changes are made, to assist managers in preparing responses to issues as they arise and help in reducing potential conflicts. For example, during this study, the eco-sensitive region of SGNP called Aarey was in the middle of a societal debate about the metro car shed which was frequently visited by leopards. By studying the perceptions and attitudes of local populations towards such developmental projects and transparently debating their impacts on the natural biodiversity, managers open a path of engagement with the community and receive critical input to inform future planning.

6.6. Conclusions

This study provides a critical discussion of multi-stakeholders' perceptions of leopards in Sanjay Gandhi National Park, Mumbai. The study shows that the seven stakeholder groups have unified perceptions towards leopards as an issue, threats towards the leopards and factors contributing to the reduction in leopard attacks. In landscapes where humans and big cats coexist, there needs to be tolerance and common goals that can safeguard both people and animals. Creating a conservation policy for such human-dominated landscapes must include the views of various stakeholders and make them the ambassadors of leopard welfare, in addition to conservation awareness and education. Thus, through the continued involvement of various stakeholders, the Forest department can further expand and generate solutions that would improve HLI in the future.

Acknowledgement

The authors would like to thank Nikit Surve for valuable discussions and for assisting in identifying the participants. We also thank Dr Delfi Chinnappan for her suggestions on the study design, Orvill Nazareth and Dr Russell Thompson on data visualisation. Lastly, we are extremely grateful to the participants who contributed to this study.

Declaration

Individual stakeholders contacted were informed of the purpose of the study and asked for permission to be surveyed.

Chapter 7: Discussion

7.1. Key Findings

Animal and human lives are interconnected and how we interact and understand endangered species, will allow us to identify and resolve the challenges faced by them. In today's modern era, many fields are merging to provide better solutions for wildlife. The application of emerging findings around animal sentience and involving various stakeholders, has provided us with tremendous information that has also prompted action in the field of animal welfare (Buller, Blokhuis, Lokhorst, Silberberg, & Veissier, 2020). However, there are few studies using such interdisciplinary approaches in other aspects of wildlife conservation. In an attempt to improve the welfare of big cats, this research has studied how dynamic fields can contribute together. Three main elements that may influence the welfare of big cats were examined: animal personality, stress physiology, and human perception of big cats.

The overall aim of this thesis was to apply non-invasive interdisciplinary approaches to improve the field of big cat welfare. It aimed to investigate; i) individual variation through the association between personality and GCs in big cats by reviewing the literature and identifying factors that influence this relationship (Chapter 2), ii) the relationship between personality and cortisol levels in captive African lions (Chapter 3), iii) the influence of social and environmental factors on the personality and cortisol levels of captive African lions (Chapter 4), iv) The potential for understanding human perception towards the welfare of captive big cats in India and Australia (Chapter 5), and v) The potential for understanding multistakeholder perception towards the welfare of wild leopards in the Sanjay Gandhi National Park, India (Chapter 6).

To conduct this research, permission was acquired from the Animal Ethics Committee at Western Sydney University (A12772), and the Biosafety and Radiation Safety Committee (B12366) to observe lions and collect biological samples, and later the Human Ethics Committee to assess the attitudes of humans. To assess these elements for improving the welfare of big cats the thesis was divided into thesis chapters with specific questions. A summary of these methods and key findings have been described in Table 7.1.

Table 7. 1 Analysis and key findings for thesis chapters

Area	Chapter	Test	Key findings
Ethology, Psychology, Physiology	2	• Conducted review analysis to establish links between personality and stress physiology in big cats	• Identified five factors that influence the integrated relationship between personality and stress
	3	• Assessed the personality and cortisol levels in captive African lions • The personality of each lion was rated using the wild cat personality checklist • The cortisol level was measured from fresh faecal samples using a commercial cortisol EIA	• A strong correlation was found between personality and cortisol in African lions • Lions with agreeable personality types had lower cortisol levels
	4	• Determined the social and environmental preferences and their links to personality and cortisol in captive African lions • Social interactions were assessed by observing lion behaviour and applying the Association Index • Environmental preferences were assessed by observing lions using the enclosure space and enrichment items and applying the Spread of Participation Index and Electivity index	• Social interactions were negatively influenced by dominant personality types • Lions rated higher on agreeableness showed some tendency to use secluded shaded areas with enrichment items
Sociology, Psychology	5	• Public attitudes towards captive big cats and their welfare were assessed using an online questionnaire in India and Australia	• The number of zoo visits influenced all parameters assessing big cat welfare • Other factors such as location, age, gender and education, and some of the interactions between these factors, also influenced several parameters measured
	6	• A questionnaire and a semi-structured interview were used to collect data on stakeholders' perception of human-leopard interactions in Sanjay Gandhi National Park, Mumbai	• There were no significant differences in the seven stakeholder group's perceptions towards leopards as an issue, in threats towards leopards of SGNP as part of the urban landscape of Mumbai, and factors resulting in the reduction of leopard attacks

7.2. Significance of this research

The contributions of multiple disciplines towards the field of wild animal welfare science are now getting well established. Charismatic big cats often get a lot of attention, yet there is very limited focus on understanding their individual responses to stressors and welfare (Torgerson-White & Bennett, 2014; Vaz, McElligott, et al., 2022). Managing big cats more effectively in captivity relies on an understanding of the stressors they face and how different individuals respond to them (Koolhaas et al., 1999). Before this thesis, the majority of the studies have studied either the personality or stress physiology of big cats, with few studies exploring this integrated relationship. Therefore, Chapter 2 is a review analysis that summarises research conducted on large felid personality and its connection to welfare over the past 33 years. Out of the 53 research articles found online, 15 focused on personality, 31 on stress physiology, and seven studies explored the relationship between personality and reaction to stressors in big cats (Bertocchi et al., 2015; DeCaluwe et al., 2013; Jurke et al., 1997; Torgerson-White & Bennett, 2014; Wielebnowski et al., 2002). Further, we identified five interlinked factors that may work together to influence the personality and stress physiology of big cats. These key factors are social interaction (Bertram, 1975; Chadwick, 2014; S. Kaiser et al., 2015), environment (Gartner et al., 2014; Torgerson-White & Bennett, 2014; Wielebnowski et al., 2002), life history and evolutionary traits (Goswami et al., 2020; Jurke et al., 1997; Wielebnowski et al., 2002), genetics (Carlstead & Shepherdson, 2000; Wielebnowski et al., 2002; Zayan, 1991), and health (Gartner et al., 2016; Gartner & Weiss, 2013b; Wielebnowski, 1999). 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. The review also compared the methods applied in assessing the personality and GC levels in big cats over the years.

From the review chapter, further linking the personality with stress physiology in big cats, the next chapter (Chapter 3) explored this integrated relationship in captive African lions. We found two personality dimensions – dominance and agreeableness among the studied captive African lions. Dominance loaded positively and strongly

for behavioural traits - erratic, bullying, defiant, irritable, bold, solitary and inventive, while the behavioural traits gentle, trusting, stable, affectionate and friendly to people loaded negatively. Similarly, previous studies rated reintroduced African lions for their boldness, another term commonly used for dominance (Dunston et al., 2016) and Asiatic lions on a bold-shy axis for comparing individuals raised in captivity and others that were wild-rescued (Goswami et al., 2020). This suggests this dimension of dominance may be a prevalent trait among lions and indicates that the social structure with roles of different individuals in a pride is important for their well-being (Gartner et al., 2016). The dimension of agreeableness, though not discussed in the past for African lions, has been discussed for other wild cats such as clouded leopards (Gartner et al., 2014) and domestic cats (Litchfield et al., 2017). Agreeableness may also be required for members of the pride to get along with each other to lead a social life. In addition, the influence of factors such as sex, location and age were strongly related to the two personality types, emphasising the social organisation of lions where males and females of different age groups play an important role in the pride (Vaz, Bartley, et al., 2022). Finally, lions rated higher for agreeableness had lower cortisol levels, highlighting that their behavioural traits help them in developing better coping strategies (Antonevich et al., 2020; Boccia et al., 1995).

Based on the findings from the previous chapters (Chapter 2 and 3), Chapter 4 assessed if the social and environmental factors contributed to the individual animal's welfare and was influencing the personality or stress physiology. Particularly, **t**he study assessed if the social interactions, enclosure usage and enrichment preference of African lions varied with their personality, cortisol levels, enclosure size and age. The results obtained showed that social interactions were negatively related to the dominance personality type. This may relate to the social structure of African lions which consists of 'fission-fusion' social units, either comprising a male with four-six related females with or without offspring, or sometimes as a coalition of unrelated males, while some others show nomadic behaviours (Schaller, 1972; Sogbohossou et al., 2014). Due to competition for resources in the wild or in an enclosure, dominant individuals are highly territorial and control resource allocation among conspecifics through dominant and territorial behaviours (Mosser & Packer, 2009; Packer et al.,

1990; Sundstrom & Altman, 1974). These dominant individuals tend to spend more time solitary without interacting with others, as compared to individuals rated for agreeableness. There was also a slight positive relationship between agreeableness and the preference for shaded areas with enrichment items, with similar findings reported for Asiatic lions (Goswami et al., 2021). While there was no preference for the stage usage, it was observed that there was a slight preference for the shade usage, especially for lions rated for agreeableness. These lions over-utilised the shaded areas more than the others. The shaded areas provide more privacy, and it appeared to be well-suited for agreeable animals who could find comfort and feel less stressed, to then go back to showing their natural behaviours (Marinath et al., 2019). These results are useful for assessing how animals share resources, interact with each other within their enclosures or may prevent the exclusion of certain members. Thus, determining the social and environmental preferences could be useful to manage lions in future ex-situ programs and could be extrapolated to other social species.

Whilst observing animals directly and using behavioural and physiological welfare indicators are important to measure their welfare, the further implementation of policies to safeguard their welfare depends on the role of society and human attitudes. To build on the work of using interdisciplinary approaches, Chapter 5 explores the current attitudes of the Indian and Australian public towards captive big cats and their welfare, and further identified the factors that may influence these attitudes. Our study specifically assessed if there were differences in the attitudes towards reasons for visiting zoos, most liked aspects of big cats, encounters with big cat management, environmental conditions preferred for big cats and big cat welfare concerns, and if these attitudes could be predicted with the location, age, gender, education, and past zoo visits of the public. Most of our predictions were confirmed by the results, with some contrasts to a few theories from previous research. For example, overall, the number of zoo visits was strongly associated with all the six constructs we used for measuring attitudes towards big cats and their welfare. While previous studies have regularly viewed attitudes to be distinct due to the influence of various factors (Kellert, 1985a), our results show a high level of association between the interactions and the factors.

Finally, this thesis would be incomplete without exploring the human dimension towards the welfare of wild big cats. Consequently, Chapter 6 was designed to assess the current stakeholders' perceptions towards leopards in the wild using a case study of the Sanjay Gandhi National Park in Mumbai, India. From the seven stakeholder groups that were assessed, the results show no significant differences in the perceptions of these stakeholder groups towards leopards as an issue, in threats towards leopards of SGNP as part of the urban landscape of Mumbai, and factors resulting in the reduction of leopard attacks. The research hypothesis that due to the interconnectedness of stakeholder groups and involvement in the park, there would be fewer differences in perceptions was supported. In addition, the previous leopard awareness workshops held by the Forest Department could have contributed to this (Ghosal, 2018). The close working relationships across the stakeholder groups, especially on HLIs and keeping up to date with the changes occurring in the park, actively contribute towards informing and sustaining the groups' similar conservation and welfare efforts. Similar studies involving local stakeholders have been successful in facilitating serious conservation management to safeguard the welfare of wild felids in various protected areas of South-east Asia (T. D. Allendorf et al., 2007; Udaya Sekhar, 2003). Thus, through the continued involvement of various stakeholders, we can further expand and generate solutions that would improve the welfare of wild cats in the future.

Overall, this work provides novel evidence suggesting that interdisciplinary approaches may be imperative to resolve and improve the welfare of big cats. The different chapters were faced with a few limitations which we have acknowledged here and under each chapter in detail. We tried addressing these limitations and recommend that future research may consider these too. Although some lions in the study of Chapter 3 and 4 were circus-raised individuals, the results may pose a limitation when compared to lions in other captive settings. However, we believe that this study has the merits to showcase positive welfare indicators by focusing on individual welfare.

In Chapter 5, since the online surveys were administered using a snowball approach, the overall reach of these surveys cannot be measured because, although it would have reached wider audiences, some may have opted not to participate. Further, these findings are species and location specific, and there is a potential for a social response bias to exist, but this may be prevented if upcoming studies could consider including items to check for a social response bias. Further, the study on human perception towards leopards in Chapter 6 brought together a wide range of individuals and organisations, yet several other relevant stakeholders such as the Police, Municipality/ City council and Fire department officials were not surveyed. It is likely their perceptions will differ from the other groups involved. Although the study aimed to have equal gender representation, the positions filled by different stakeholders included a much higher representation of men which suggests the cultural influences of the study location. We also aimed to survey higher sample size, but this was not possible in this study due to the case study being based on one scenario. Lastly, due to impacts of COVID 19 restrictions, we couldn't interview all the stakeholders on field as planned, and organised online Zoom interviews for those participants who agreed to participate.

7.3. Future directions and research perspectives

The work in this thesis provides an understanding of the current trends in using integrated approaches and has further contributes to the field of big cat welfare. We also raise questions that some of these studies should tackle and suggest broader applications of this research. The work in this thesis provides a road map for future studies expanding on the big cat welfare. 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. As many captive big cats are part of conservation breeding programmes, future studies integrating personality and GC levels 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. Similarly, the ongoing narratives of sharing spaces with big cats in the wild requires a holistic approach and understanding of human perceptions towards these debates.

We suggest developing and incorporating a more systematic approach to the management of individual lions or big cats in zoos, rescue centres or reintroduction programs. Maintaining a repository of the personality profiles of big cats' can be valuable for big cats' caretakers to enhance their knowledge of animals in their care and/or implement interventions such as veterinary assessments or enclosure developments. The big cat managers can collate personality and stress-related endocrine data collected from their animals into the Zoological Information Management Software (ZIMS), so it is accessible to other big cat caretakers around the world. Even though it is expected that the reported GC concentrations would have resulted from different methodologies in sample collection; extraction and analysis, the storing of this data in a single online database will help to compare and contrast the methods and further refine the technique beneficial for big cats. This would assist in understanding factors influencing personality and GC levels, and help improve individual and thus overall welfare for big cats.

We also recommend conducting a biological validation before using every commercial kit, which may be conducted by using samples from a naturally occurring stressful event, such as the introduction of a new individual to the group, or translocation from one enclosure to another. The advantages of this study can then be applied to tailor animal welfare management specific to individual variation. For example, providing felids rated high on agreeableness with good hiding spots could reduce the impact of stressors, as seen among cheetahs rated on tense-fearful scores or among jungle cats with lower corticosterone levels (Marinath et al., 2019; Wielebnowski, 1999). In addition, a less-agreeable cat with higher GC levels may need those hiding spots even more. Thus, this information is also beneficial in exhibit design, conservation reintroduction programs, and species survival recovery plans to incorporate the needs while bringing a group of social animals together.

Positive welfare can further be improved by understanding the preferences and how an animal feels in its environment. Providing lions rated higher on agreeableness with continuous access to a shaded area with some privacy may suit their needs. Knowledge about a lion's preferences can be extremely useful in reintroduction programs, where animals may be selected and kept in a pre-release facility to encourage bonding with unfamiliar individuals to form cohesive groups in unfamiliar surroundings. In addition, assessing the unique personality traits within the group and providing various enrichment interventions specific to these individual differences can be useful to the big cats' welfare. More recently, the University of Birmingham in partnership with local zoos designed an interactive interface - The Enclosure Design Tool for apes and parrots to compare the behaviour of captive or rescued individuals to those of their wild peers, which will be beneficial to apply across other species in future. By using such tools, there is scope to design complex enclosures with a natural social structure to suit individual animals' preferences. For example, assessing a lion's personality can provide insights for establishing compatible groups and further introduce enrichment items that would promote their welfare, such as hiding spots or exposed heights. We also suggest that upcoming studies could focus on having a strong demographic representation of prides with comparable size and age groups to expand on this study.

Further, as humans with positive attitudes towards preferred species are likely to show more care and concern towards their welfare, future research can investigate the social, cultural, and political factors according to the study locations. Also at a community level, zoos could take additional efforts to evaluate the views of their visitors about their animals using trialled approach such as the practical I-Change model which measured the efficacy of the interactive TigerTrek Exhibit at Taronga Zoo in influencing visitors' tiger conservation attitudes and behaviours (Kelly & Skibins, 2021). By incorporating such models using modern technology with the assessment of demographic factors, zoos could reach wider audiences on a long-term basis. Thus, attitudes towards big cats and their welfare are complex and may be influenced by various individual or integrated factors, and zoos represent opportunities in educating the general public.

To improve the welfare of wild big cats, our discussions with the stakeholder groups indicate several areas can be developed to enhance the current situation and practices. We advocate appropriately using multilingual modes of communication to reach larger audiences as a priority to garner wider interest and support in actively protecting the parks and their leopards. In the case of protecting forests like SGNP, we advocate developing a legal policy that safeguards the forests from future developmental projects. Such a policy will protect the biodiversity and habitat of leopards along with the land of the indigenous and non-indigenous residents. Linking the policies of the park with the global Aichi Biodiversity Targets such as Strategic Goal E: Enhance implementation through participatory planning, knowledge management and capacity building, will further strengthen the commitment of SGNPs' stakeholders to protecting the park and its inhabitants, both human and wild animals. Similarly, their relevance also applies by implementing the PARTNERS principles to improve human-animal relationships through community participation, which could be a great model for SGNP stakeholders to work together. These partnerships may help in applying traditional knowledge aimed at protecting the forest and achieving wider social and environmental outcomes, keeping the encroachers away. We also recommend conducting a stakeholder analysis after any new management interventions or policy changes are made, to assist managers in preparing responses to issues as they arise and help in reducing potential conflicts. By studying the perceptions and attitudes of local populations towards such developmental projects and transparently debating their impacts on the natural biodiversity, managers open a path of engagement with the community and receive critical input to inform future planning. Thus, these recommendations can be implemented across various managements that oversee big cats such as zoos, rescue centres, reintroduction programs or wild habitats.

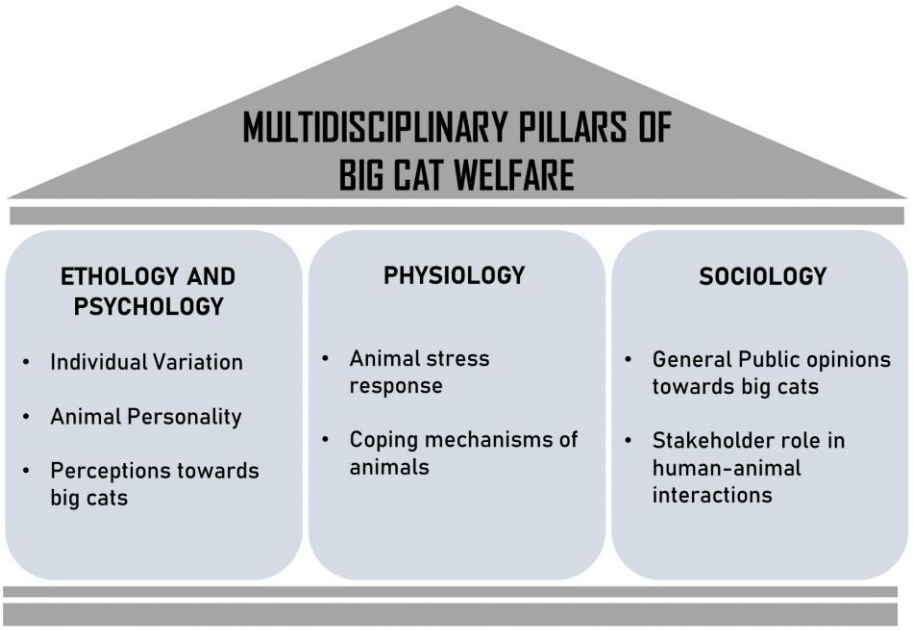

Figure 7. 1 Framework of interdisciplinary approaches applied to the field of big cat welfare

Overall, this thesis takes an interdisciplinary approach (Figure 7.1) to incorporate and link the fields of physiology, psychology, and sociology to improve the welfare of big cats in captivity and the wild. By intersecting these three fields, our studies emphasize understanding the most effective ways and have identified methods that can be replicated in captive or wild settings to improve the welfare of big cats.

Appendices

Appendix A – Chapter 2 Supplementary material

Table S2. 1 Summary of published and unpublished research on big cat personality and stress physiology

Big cat Personality					
Author	**Species**	**Sample Size**	**Origin**	**Methodology**	**Factors discussed**
(Antonevich et al., 2020)	Eurasian lynx	45	Captive	Behavioural observation	Social interaction, Health
(Goswami et al., 2020)	Asiatic lion	35	Captive	Novel object/ Keeper survey	Social Interaction
Wang et al. (2019)	Amur tiger	45	Captive	Behavioural observation/ Keeper survey	Genetics, Health
(Boccacino et al., 2018)	Jaguar	4	Captive	Behavioural observation	Environment, Health
Kamyk (2017)*	African lion	12	Reintroduced§	Novel object	Social Interaction, Environment
(Pastorino, Viau, et al., 2017)	Asiatic lion	4	Captive	Keeper survey	Social Interaction, Environment
	Tiger	9	Captive		
(Phillips et al., 2017)	Cheetah	4	Captive	Keeper survey	Social Interaction, Environment
(Pastorino, Paini, et al., 2017)	Tiger	8	Captive	Behavioural observation/Keeper survey	Social Interaction, Health
(Dunston et al., 2016)	African lion	11	Reintroduced§	Novel object/ Behavioural observation	Social Interaction, Environment
(Gartner et al., 2014)	African lion	21	Captive	Keeper survey	Social Interaction, Genetics, Health
	Snow leopard	17	Captive		
(Chadwick, 2014)*	Cheetah	37	Captive	Behavioural observation	Social Interaction, Environment, Genetics, Health
(Baker & Pullen, 2013)	Cheetah	35	Captive	Novel object/ Behavioural observation	Social Interaction, Environment
(Gartner & Powell, 2012)	Snow leopard	10	Captive	Keeper survey/ Novel object	Environment, Genetics

(Phillips & Peck, 2007)	Royal Bengal tiger	7	Captive	Keeper survey	Social Interaction, Environment, Genetics
(Wielebnowski, 1999)	Cheetah	44	Captive	Keeper survey/ Behavioural observation	Social Interaction, Environment, Genetics

Big cat Stress Physiology

Author	Species	Sample Size	Origin	Methodology	Factors discussed
(Azevedo et al., 2020)	Iberian lynx	12	Captive, Wild	Hair cortisol & corticosterone metabolite EIA	—
(Burstahler, Terwissen, & Roth, 2019)	Canada lynx		Wild harvest	Hair cortisol metabolite EIA	Environment
(Naidenko, Berezhnoi, Kumar, & Umapathy, 2019)	Amur tiger Royal Bengal tiger	-- --	Wild Wild	Faecal cortisol metabolite EIA	--
(Sgambelluri, 2018)*	African lion	2	Captive	Saliva corticosterone metabolite EIA	Social Interaction, Environment, Genetics, Health
(Webster, Burroughs, Laver, & Ganswindt, 2018)	African leopard	7	Captive & Wild	Faecal cortisol, corticosterone metabolites EIA	Environment, Life History and Evolutionary traits
(Malviya et al., 2018)	Royal Bengal tiger	--	Wild	Faecal cortisol metabolite EIA	Environment, Genetics, Health
(Vaz et al., 2017)	Royal Bengal tiger Indian Leopard	18 9	Captive Captive	Faecal corticosterone metabolite EIA	Social Interaction, Environment, Health
(Ivanov, Rozhnov, & Naidenko, 2017)	Amur tiger	3	Captive	Faecal cortisol metabolite EIA	Environment
(Mesa-Cruz et al., 2016)	Jaguar Puma	-- --	Wild Wild	Faecal corticosterone metabolite RIA	Genetics, Health
(Bhattacharjee et al., 2015)	Royal Bengal tiger	5	Wild	Faecal cortisol metabolite EIA	Environment, Life History and Evolutionary traits, Health
(Pavlova et al., 2015)	Amur leopard	--	Wild	Faecal cortisol metabolite EIA	Social Interaction, Environment, Health
(Parnell et al., 2014)	Sumatran tiger	5	Captive	Faecal cortisol metabolite EIA	Social Interaction,

					Environment, Genetics, Health
(Mesa-Cruz et al., 2014)	Jaguar	10	Wild	Faecal cortisol metabolite EIA /corticosterone metabolite RIA	Environment
(Pribbenow et al., 2014)	Eurasian lynx Iberian lynx	3 5	Captive	Faecal cortisol & corticosterone metabolite EIA	Environment
(Fanson & Wielebnowski, 2013)	Canada lynx	45	Captive	Faecal corticosterone metabolite EIA	Social interaction, Environment
(Ludwig et al., 2013)	Cheetah	7	Captive	Faecal corticosterone metabolite EIA	—
(Terwissen, Mastromonaco, & Murray, 2013)	Canada lynx	3	Captive	Hair cortisol metabolite EIA	Health
(Watson et al., 2013)	Amur leopard Amur tiger Cheetah Snow leopard Sumatran tiger	2 2 2 2 1	Captive Captive Captive Captive Captive	Faecal corticosterone metabolite EIA	--
(Narayan et al., 2013)	Sumatran tiger Royal Bengal tiger	11 11	Captive Captive	Faecal cortisol metabolite EIA	Social Interaction, Environment, Health
(S Creel et al., 2013)	African lion	34	Wild	Faecal cortisol metabolite EIA	Social Interaction
(Conforti et al., 2012)	Jaguar	16	Captive	Faecal cortisol metabolite RIA	Environment, Health
(Fanson, Wielebnowski, Shenk, & Jeffrey, 2012)	Canada lynx	39 135	Captive Wild	Faecal cortisol & corticosterone metabolite EIA	Life history and Evolutionary traits
(Burgener et al., 2008)	Snow leopard	2	Captive	Faecal cortisol metabolite EIA	Social Interaction, Environment
(Schildkraut, 2016)*	African lion	9	Captive	Faecal and hair corticosterone metabolites EIA	Social Interaction, Environment, Health
(Dembiec, Snider, & Zanella, 2004)	Tiger	5	Captive	Faecal cortisol metabolite RIA	Environment,
(Young et al., 2004)	Cheetah	2	Captive	Faecal cortisol metabolite EIA/ corticosterone metabolite RIA	Social Interaction, Environment, Genetics
(Terio et al., 2004)	Cheetah	40	Captive & Wild	Faecal cortisol metabolite RIA	Social Interaction,

					Environment, Health
(Nogueira & Silva, 1997)	Jaguar	8	Captive	Blood cortisol metabolite RIA	Environment
	Cougar	13	Captive		
(Wildt et al., 1988)	Cheetah	3	Captive	Blood cortisol metabolite RIA	Environment, Genetics, Health
	Tiger	7	Captive		
	Leopard	4	Captive		
	Puma	3	Captive		
(J. L. Brown et al., 1988)	Tiger	3	Captive	Blood cortisol metabolite RIA	Genetics
	North Chinese leopard	6	Captive		
(Wildt et al., 1987)	Cheetah	31	Captive & Wild	Blood cortisol metabolite RIA	Environment, Life History and Evolutionary traits, Genetics

Big Cat Personality and Stress Physiology

Author	Species	Sample size	Origin	Methodology	Factors discussed
(Razal et al., 2016)	African cheetah	17	Captive	Behavioural observation, Keeper survey / Faecal corticosterone metabolite RIA	Social Interaction
(L. J. Miller, Pisacane, & Vicino, 2016)	Cheetah	18	Captive	Behavioural observation, Keeper survey / Faecal corticosterone metabolite RIA	Social Interaction, Environment
(Bertocchi et al., 2015)	Amur tiger	2	Captive	Behavioural observation/ Faecal Cortisol metabolite EIA	Social Interaction, Environment
(Torgerson-White & Bennett, 2014)	African lion	6	Captive	Keeper survey / Faecal corticosterone metabolite RIA	Social Interaction, Environment
(DeCaluwe et al., 2013)	Clouded leopard	16	Captive	Keeper survey / Faecal cortisol metabolite EIA	Environment
(Wielebnowski et al., 2002)	Clouded leopard	72	Captive	Keeper survey / Faecal corticosterone metabolite RIA	Environment, Health
(Jurke et al., 1997)	Cheetah	7	Captive	Keeper survey / Faecal cortisol metabolite RIA	Social Interaction, Environment, Genetics

*Thesis/ unpublished work; Reintroduced§ = Reintroduced animals from captivity to wild;
EIA = Enzyme immunoassay, RIA = Radioimmunoassay

Appendix B – Chapter 3 Supplementary material

Table S3. 1 Demography of lions studied at our two study sites

Study Site	Lion	Sex	Age	Weight (kg)	Origin (zoo/ circus)	Distribution *	Faecal samples per lion	Average Cortisol (ng/g)	Enclosure size (sq.m.)
1	1	Male	7	220	Zoo	Pride	3	0.199	900
	2	Female	16	160	Zoo	Pride	2	0.203	900
	3	Female	16	160	Zoo	Pride	1	0.192	900
	4	Male	16	180	Zoo	Pair	2	0.209	300
	5	Female	11	160	Zoo	Pair	3	0.195	300
	6	Male	5	210	Zoo	Pride	3	0.204	900
	7	Female	6	160	Zoo	Pride	3	0.197	900
	8	Female	6	160	Zoo	Pride	2	0.202	900
	9	Female	5	160	Zoo	Pride	2	0.181	900
	10	Male	11	180	Zoo	Pride	2	0.21	900
	11	Female	11	160	Zoo	Pride	3	0.201	900
	12	Male	5	170	Zoo	Pride	1	0.211	900
	13	Male	12	170	Circus	Bachelor	2	0.207	400
	14	Male	12	170	Circus	Bachelor	2	0.204	400
	15	Male	5	160	Zoo	Solitary	3	0.206	300
	16	Female	15	160	Circus	Pride	1	0.202	220
	17	Male	15	180	Circus	Pride	2	0.202	220
	18	Female	15	180	Circus	Pride	1	0.203	220
2	19	Male	3	217	Zoo	Bachelor	1	0.191	1500
	20	Male	3	197	Zoo	Bachelor	3	0.204	1500
	21	Male	3	202	Zoo	Bachelor	3	0.204	1500
	22	Male	3	230	Zoo	Bachelor	1	0.183	1500

*Distribution indicates animals living as solitary, pair, male bachelor group or pride

Table S3. 2 The Intra-class Correlation Coefficients (ICC) were used to measure the reliability of different raters. Thirty-four unreliable behavioural traits with ICC scores lower than 0.75 and Class Intervals overlapping 0 were excluded, and 18 behavioural traits passed the reliability test (in bold).

Traits	Location 1			Location 2		
	ICC (3,k)	**Lower CI**	**Upper CI**	**ICC (3,k)**	**Lower CI**	**Upper CI**
Active	**0.8**	**0.61**	**0.91**	**0.95**	**0.74**	**0.99**
Affectionate	**0.92**	**0.85**	**0.96**	**0.89**	**0.49**	**0.99**
Aggressive to conspecifics	0.72	0.46	0.87	0.8	0.066	0.98

Aggressive to people	0.72	0.46	0.87	0.94	0.7	0.99
Aimless	0.7	0.421	0.86	0.89	0.471	0.99
Anxious	0.43	-0.108	0.73	0.95	0.78	0.99
Bold	**0.82**	**0.65**	**0.91**	**0.81**	**0.073**	**0.98**
Bullying	**0.85**	**0.71**	**0.93**	**0.88**	**0.41**	**0.99**
Calm	0.63	0.29	0.83	0.8	0.039	0.98
Clumsy	**0.88**	**0.77**	**0.95**	**0.76**	**-0.1266**	**0.97**
Constrained	0.67	0.356	0.84	0.72	-0.332	0.97
Cool	0.75	0.51	0.88	0.92	0.6	0.99
Cooperative	0.65	0.325	0.84	0.79	0.0068	0.98
Curious	0.54	0.036	0.78	0.78	-0.0273	0.98
Decisive	0.58	0.181	0.8	0.83	0.168	0.98
Defiant	**0.85**	**0.7**	**0.93**	**0.88**	**0.44**	**0.99**
Deliberate	0.79	0.6	0.9	0.7	-0.437	0.97
Distractible	**0.85**	**0.71**	**0.93**	**0.88**	**0.45**	**0.99**
Dominant	0.87	0.74	0.94	0.72	-0.338	0.97
Eccentric	0.83	0.67	0.92	0.68	-0.529	0.96
Erratic	**0.99**	**0.97**	**0.99**	**0.94**	**0.73**	**0.99**
Excitable	0.88	0.76	0.94	0.73	-0.297	0.97
Fearful of conspecific	0.63	0.279	0.82	0.6	-0.9	0.96
Fearful of People	0.308	-0.337	0.67	0.99	0.93	1
Friendly to Conspecifics	0.79	0.59	0.9	0.75	-0.189	0.97
Friendly to People	**0.91**	**0.83**	**0.96**	**0.89**	**0.47**	**0.99**
Gentle	**0.86**	**0.73**	**0.93**	**0.92**	**0.61**	**0.99**
Impulsive	0.81	0.63	0.91	0.651	-0.662	0.96
Independent	0.64	0.302	0.83	0.95	0.77	0.99
Individualistic	0.79	0.6	0.9	0.75	-0.189	0.97
Inquisitive	**0.82**	**0.65**	**0.91**	**0.88**	**0.415**	**0.99**
Insecure	0.484	0.0032	0.76	0.93	0.66	0.99
Inventive	**0.79**	**0.59**	**0.9**	**0.94**	**0.72**	**0.99**
Irritable	**0.89**	**0.79**	**0.95**	**0.89**	**0.46**	**0.99**
Jealous	0.81	0.64	0.91	0.68	-0.503	0.96
Persevering	0.69	0.4	0.85	0.67	-0.586	0.96
Playful	**0.9**	**0.8**	**0.95**	**0.86**	**0.347**	**0.98**
Predictable	0.71	0.438	0.86	0.65	-0.66	0.96
Quitting	0.66	0.348	0.84	0.75	-0.189	0.97
Reckless	0.88	0.76	0.94	0.68	-0.508	0.96
Self-assured	0.426	-0.111	0.73	0.66	-0.61	0.96
Smart	0.7	0.41	0.86	0.87	0.37	0.99
Solitary	**0.9**	**0.8**	**0.95**	**0.83**	**0.192**	**0.98**
Stable	**0.91**	**0.83**	**0.96**	**0.8**	**0.049**	**0.98**
Stingy	0.84	0.69	0.92	0.74	-0.232	0.97
Submissive	0.79	0.6	0.9	0.74	-0.235	0.97

Suspicious	0.65	0.325	0.84	0.66	-0.605	0.96
Tense	0.62	0.256	0.82	0.93	0.68	0.99
Timid	0.61	0.242	0.82	0.63	-0.74	0.96
Trusting	**0.76**	**0.54**	**0.89**	**0.91**	**0.55**	**0.99**
Vigilant	0.55	0.122	0.79	0.9	0.539	0.99
Vocal	**0.82**	**0.65**	**0.92**	**0.99**	**0.95**	**1**

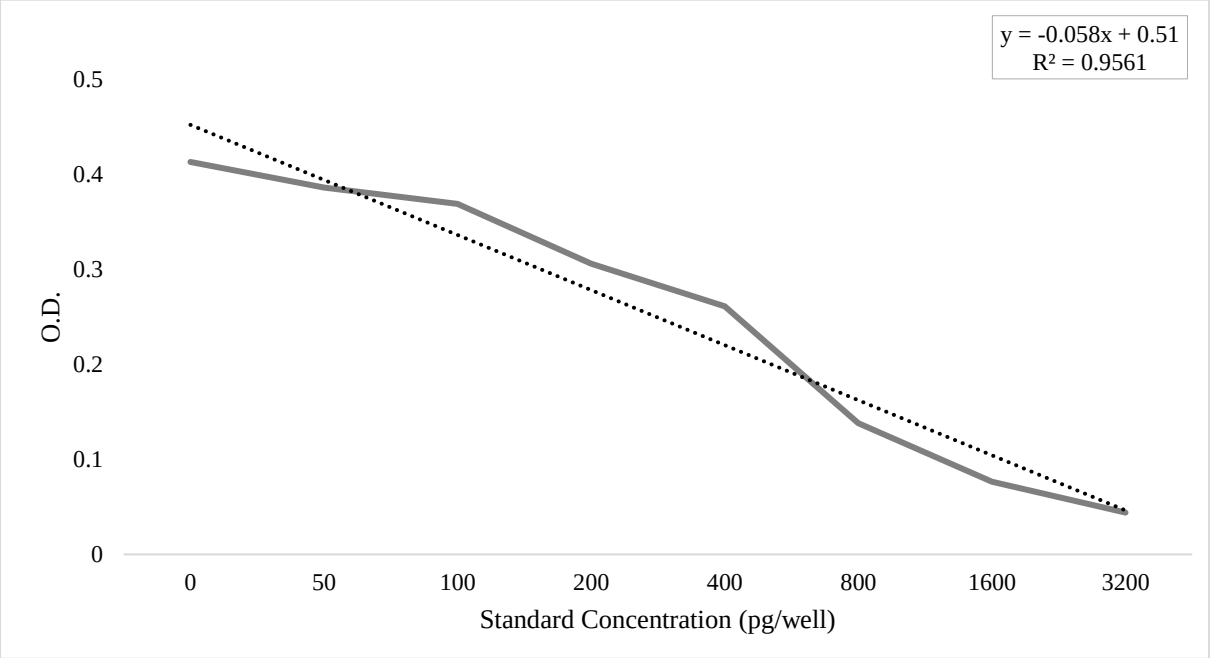

Figure S3. 1 Regression plot for cortisol standard in the extract pool (extraction efficiency = 95%)

Table S3. 3 Parallel analysis showing the reduction of four Principal Components (PCs) from our unrotated PCA to two PCs. PCs are considered significant (in bold) in parallel analysis when the raw data for an eigenvector (root) exceeds the mean value for that eigenvector.

Root	Raw Data	Means	Percentile	Significant Principal Components
1.000000	**6.831026**	3.057763	3.505020	PC1 - Dominance
2.000000	**4.507664**	2.536895	2.849656	PC2 - Agreeableness
3.000000	1.728087	2.165428	2.400144	
4.000000	1.429173	1.858596	2.072662	
5.000000	.770636	1.592165	1.778667	
6.000000	.637314	1.365494	1.529774	
7.000000	.521530	1.160405	1.325590	
8.000000	.337120	.975040	1.124383	
9.000000	.313899	.816704	.950049	
10.000000	.275559	.664730	.780072	
11.000000	.241434	.531960	.649359	
12.000000	.147397	.417716	.520334	
13.000000	.112362	.313611	.405348	
14.000000	.081452	.226160	.305640	
15.000000	.025341	.153514	.219688	
16.000000	.022564	.095675	.149537	
17.000000	.013061	.050086	.091543	
18.000000	.004380	.018057	.040050	

Appendix C – Chapter 4 Supplementary material

Table S4. 1 Unrotated Principal Component Analysis of behavioural traits in African lions

While the original PCA revealed four PCs with eigenvalues greater than 1, parallel analysis reduced this to the first two PCs (Vaz, Bartley, et al., 2022).

	PC1 Dominance	**PC2 Agreeableness**
Eigenvalue	6.831	4.508
% Variance	37.950	25.043
Loadings		
Active	0.245	**0.794**
Affectionate	**-0.702**	**0.457**
Bold	**0.500**	0.380
Bullying	**0.830**	0.123
Clumsy	0.238	**0.476**
Defiant	**0.653**	0.296
Distractible	0.225	**0.837**
Erratic	**0.902**	0.111
Friendly to people	**-0.666**	0.539
Gentle	**-0.922**	0.122
Inquisitive	-0.013	**0.810**
Inventive	**0.496**	**0.668**
Irritable	**0.858**	-0.123
Playful	0.074	**0.884**
Solitary	**0.484**	0.110
Stable	**-0.775**	0.299
Trusting	**-0.869**	0.382
Vocal	0.347	-0.170

PC1 had an eigenvalue of 6.83 and explained 37.95% of the cumulative variance in the data representing a dominance axis. The traits erratic, bullying, defiant, irritable, bold, solitary and inventive loaded strongly and positively, while the traits gentle, trusting, stable, affectionate and friendly to people loaded negatively (Table S1). Hence, lions having higher PC1 scores were bolder compared to those with lesser scores, indicating more dominant individuals.

PC2 had an eigenvalue of 4.50, which explained 25.04% of the variance in the data representing an agreeableness axis. The traits of being playful, distractible, inquisitive, active, inventive, friendly to people, clumsy and affectionate loaded strongly and positively (Table S1). Hence, animals with higher PC2 scores were more agreeable, and those that scored low were more antagonistic. Based on the pattern of factor loadings, the two PCs were labelled as dominance, and agreeableness, respectively (John & Srivastava, 1999).

Table S4. 2 Summary of demography, personality, stress physiology and enclosure size for observed lions

Study Site	Lion	Sex	Age	Weight (kg)	Origin (zoo/ circus)	Dominance	Agreeableness	Cortisol (ng/g)	Enclosure size (sq.m.)
1	1	Male	7	220	Zoo	2.058	-0.021	0.199	900
	2	Female	16	160	Zoo	-0.692	-0.988	0.203	900
	3	Female	16	160	Zoo	-0.899	-1.012	0.192	900
	4	Male	16	180	Zoo	-0.128	-0.199	0.209	300
	5	Female	11	160	Zoo	-0.286	1.165	0.195	300
	6	Male	5	210	Zoo	-1.346	0.362	0.204	900
	7	Female	6	160	Zoo	-0.972	0.21	0.197	900
	8	Female	6	160	Zoo	0.136	1.024	0.202	900
	9	Female	5	160	Zoo	-0.049	1.978	0.181	900
	10	Male	11	180	Zoo	0.486	-1.393	0.21	900
	11	Female	11	160	Zoo	-0.794	-1.379	0.201	900
	12	Male	5	170	Zoo	2.105	-0.719	0.211	900
	13	Male	12	170	Circus	-0.389	-0.445	0.207	400
	14	Male	12	170	Circus	1.659	-0.369	0.204	400
	15	Male	5	160	Zoo	0.534	-0.224	0.206	300
	16	Female	15	160	Circus	-0.931	-1.286	0.202	220
	17	Male	15	180	Circus	-0.481	-0.102	0.202	220
	18	Female	15	180	Circus	-1.166	-0.146	0.203	220
2	19	Male	3	217	Zoo	1.071	0.201	0.191	1500
	20	Male	3	197	Zoo	0.101	1.981	0.204	1500
	21	Male	3	202	Zoo	0.493	-0.075	0.204	1500
	22	Male	3	230	Zoo	-0.51	1.437	0.183	1500

Table S4. 3 Electivity index (EI) values across different enrichment items for African lions

Lion	Den	Log	Log to climb	Reel	Rock	Shade	Stage	Scratch log	Toy	Tree	Tyre
1	*	-1	-1	-1	*	-1	-1	*	*	*	0.71429
2	*	-1	-1	-1	*	-1	0.68	*	*	*	-0.1429
3	*	-1	-1	-1	*	-0.0954774	0.67608	*	*	*	-1
4	*	*	-1	*	*	-0.6187514	0.70434	-1	-1	-1	*
5	*	*	-1	*	*	-0.4466301	0.69777	-1	-1	-1	*
6	-1	-1	*	-1	-1	0.0515039	0.77506	-1	-1	*	-1
7	0.41107	0.73698	*	-1	-1	-1	-1	-1	-1	*	-1
8	0.06817	0.460648	*	-1	0.46311	-0.4072055	0.33313	-1	-1	*	-1
9	-1	-1	*	-1	-1	0.0724073	-0.417	0.76282	-1	*	-1
10	*	-1	-1	-1	*	-0.4705882	0.6988	*	*	*	-1
11	*	-1	-1	-1	*	-1	0.71429	*	*	*	-1
12	*	-1	-1	-1	*	-1	0.71429	*	*	*	-1
13	*	0.348315	-1	*	*	-1	0.31765	*	*	*	*
14	*	-1	-1	*	*	0.025641	0.49333	*	*	*	*
15	*	-1	-1	*	-1	-0.3527446	0.25753	*	0.585733	*	*
16	*	*	-1	*	*	-1	0.2	*	-1	-1	0.63636
17	*	*	-1	*	*	-1	0.71429	*	-1	-1	-1
18	*	*	-1	*	*	-1	0.70971	*	-1	-0.801105	-1
19	0.78152	-1	-1	*	-1	-1	-0.1595	-1	-1	-0.784431	*
20	-1	-1	-1	*	0.485	0.6149533	-1	-1	-1	0.3156146	*
21	-1	-1	-1	*	0.59356	0.362776	0.49246	-1	-1	-1	*
22	-1	-1	-1	*	-1	0.5211268	-1	-1	-1	0.7068966	*

**Indicates enrichment item was not present in lion's enclosure; (Values between 0 and +1 = over-utilization, −1 and 0 = Under-utilization*

Table S4. 4 Summary of the response variables (AI, SPI and EI)

Lion	AI	SPI	EI (stage)	EI (shade)
1	0.33	0.49	-1	-1
2	0.71	0.47	0.68	-1
3	0.63	0.44	0.68	-0.1
4	0.54	0.5	0.7	-0.62
5	0.54	0.59	0.7	-0.45
6	0.67	0.5	0.78	0.05
7	0.63	0.58	-1	-1
8	0.63	0.46	0.33	-0.41
9	0.67	0.64	-0.42	0.07
10	0.75	0.47	0.7	-0.47
11	0.92	0.62	0.71	-1
12	0.75	0.62	0.71	-1
13	0.38	0.54	0.32	-1
14	0.38	0.48	0.49	0.03
15	**	0.69	0.26	-0.35
16	0.46	0.45	0.2	-1
17	0.46	0.66	0.71	-1
18	0.75	0.57	0.71	-1
19	0.25	0.91	-0.16	-1
20	0.79	0.7	-1	0.61
21	0.83	0.67	0.49	0.36
22	0.88	0.76	-1	0.52

**** indicates analysis without Lion #15

Table S4. 5 Correlation matrix between response variables

Response variables	AI	SPI	EI (stage)	EI (shade)
AI	1	0.064	0.061	0.401
SPI	0.064	1	-0.361	0.162
EI (stage)	0.061	-0.361	1	-0.251
EI (shade)	0.401	0.162	-0.251	1

Abbreviations: AI = Association Index, SPI = Spread of Participation Index, EI = Electivity Index

Appendix D – Chapter 5 Supplementary material

Table S5. 1 Qualtrics questionnaire used to survey participants

Title: Public attitudes towards the welfare of captive big cats in Indian and Australian zoos

Introductory Information and Consent

Part 1 Demographic questions

1. What is the postcode for where you live?
   _____

2. How long have you lived in India/Australia?
- Less than 5 years
- 5- 10 years
- 11 – 20 years
- More than 20 years

3. Age
- 18-30 years
- 31-40 years
- 41-50 years
- 51-60 years
- 61-70 years and above

4. Gender _____

5. Education level
- Grade 12 and below
- Diploma or Trade
- Bachelor's degree
- Master's degree or higher

6. Past zoo visits
- < 5 times
- 5-10 times
- 10 times

7. Closed ended questions with Yes/No responses
- Do you own/owned pets?
- Do you have children?
- Have you worked with animals?
- Would you visit a zoo in future?

Part 2 Attitudes towards big cats and welfare

1.1.1.1 *Please rate the extent to <u>which you agree</u>:*

Q1 Reasons for visiting zoos
- Seeing rare and endangered animals such as big cats
- Spending time with family or friends
- Being entertained or impressed by big cats
- Enjoying a pleasant outdoor environment
- Learning about general wildlife conservation
- Learning about big cat conservation

Q2 Most liked aspects of big cats
- Colours/coat patterns
- Hunting skills
- Size
- Unique feline behaviours
- Worship some/all big cats as deity
- Roar/Purr
- Cubs
- Whole animal

Q3 Encounters with big cats
- Walking with big cats
- Feeding big cats
- Posing with big cats or their cubs
- Playing with big cats or their cubs
- Behind the scenes for a closer look
- Selfies with big cats
- Use safari buses to view big cats without direct contact
- Live video streaming of big cats

Q4 Environmental conditions for big cats
- Large green enclosures
- Varied enrichment items
- Social animals kept in social groups (such as lions in a pride) and solitary animals (such as tigers) alone
- Hiding spots for big cats
- Enough space between different cat enclosures
- Safe and quiet environment
- Balanced/Controlled visitor numbers
- Visiting accredited zoos that follow national or state guidelines

Q5 Interactions with big cat management

- Attending keeper talks
- Visit the animal hospital at the zoo if permitted
- Participating in research/Volunteering opportunities at zoo
- Talking to keepers about their big cats well-being
- Buying gift certificates to adopt rescued/injured big cats
- Partnering with zoos for CSR (Corporate Social Responsibility) projects
- Undertaking fund raising events for rescued big cats (e.g. bake, art or photograph sale, etc.)
- Donating to zoos' partnerships to support big cats in the wild

Q6 Big cat welfare concerns

- Feeding live prey to big cats
- Captive breeding should be limited to reintroduction programs only
- Boredom affects big cats
- Selective breeding affects conservation (eg. white tigers, white lions & black leopards)
- Culling of big cats involved in incidents
- Private ownership of big cats
- It is okay to have injured/old big cats in zoos/rescue centres
- Big cats should only be bred in their native country for the purpose of conservation

1.1.1.2 *Please feel free to make any other comments about your experiences with big cats and zoos*

_____

If you would like the researcher to contact you with the results of this study, please leave your email below (optional)
You will not identified through these answers and your personal information will not be used for any other purpose.

End of Survey - Thank you.

Table S5. 2 Univariate ANOVAs were used to determine how each subscale contributed to the overall construct - Reasons for visiting zoos

Model terms	Univariate ANOVAs (Attitudes)	df	*F*	*P*
L	Q1.1-Seeing rare and endangered animals such as big cats	1, 359	0.034	0.854
	Q1.2- Spending time with family or friends	1, 359	0.088	0.766
	Q1.3- Being entertained or impressed by big cats	1, 359	0.019	0.889
	Q1.4- Enjoying a pleasant outdoor environment	1, 359	0.545	0.461
	Q1.5- Learning about general wildlife conservation	1, 359	0.008	0.929
	Q1.6- Learning about big cat conservation	1, 359	5.483	**0.02**
A	Q1.1-Seeing rare and endangered animals such as big cats	4, 359	0.431	0.787
	Q1.2- Spending time with family or friends	4, 359	2.726	**0.029**
	Q1.3- Being entertained or impressed by big cats	4, 359	1.655	0.16
	Q1.4- Enjoying a pleasant outdoor environment	4, 359	1.172	0.323
	Q1.5- Learning about general wildlife conservation	4, 359	1.333	0.257
	Q1.6- Learning about big cat conservation	4, 359	0.88	0.476
G	Q1.1-Seeing rare and endangered animals such as big cats	1, 359	3.072	0.081
	Q1.2- Spending time with family or friends	1, 359	3.335	0.069
	Q1.3- Being entertained or impressed by big cats	1, 359	1.985	0.16
	Q1.4- Enjoying a pleasant outdoor environment	1, 359	1.952	0.163
	Q1.5- Learning about general wildlife conservation	1, 359	1.326	0.25
	Q1.6- Learning about big cat conservation	1, 359	11.238	**0.001**
E	Q1.1-Seeing rare and endangered animals such as big cats	3, 359	0.693	0.56
	Q1.2- Spending time with family or friends	3, 359	0.473	0.701
	Q1.3- Being entertained or impressed by big cats	3, 359	1.758	0.155
	Q1.4- Enjoying a pleasant outdoor environment	3, 359	0.375	0.771
	Q1.5- Learning about general wildlife conservation	3, 359	0.476	0.699
	Q1.6- Learning about big cat conservation	3, 359	2.55	0.056
Z	Q1.1-Seeing rare and endangered animals such as big cats	2, 359	8.612	**0.00**
	Q1.2- Spending time with family or friends	2, 359	1.109	0.331
	Q1.3- Being entertained or impressed by big cats	2, 359	0.88	0.416
	Q1.4- Enjoying a pleasant outdoor environment	2, 359	0.288	0.75
	Q1.5- Learning about general wildlife conservation	2, 359	1.439	0.239
	Q1.6- Learning about big cat conservation	2, 359	2.251	0.107
L X A	Q1.1-Seeing rare and endangered animals such as big cats	4, 359	2.842	**0.024**
	Q1.2- Spending time with family or friends	4, 359	1.769	0.134
	Q1.3- Being entertained or impressed by big cats	4, 359	3.513	**0.008**

	Q1.4- Enjoying a pleasant outdoor environment	4, 359	1.381	0.240
	Q1.5- Learning about general wildlife conservation	4, 359	0.710	0.585
	Q1.6- Learning about big cat conservation	4, 359	2.965	**0.020**

'X' represents an interaction between independent variables. Boldface represents a significant difference (P = <0.05)

Table S5. 3 Univariate ANOVAs were used to determine how each subscale contributed to the overall construct - most liked aspects of big cats

	Univariate ANOVAs			
Model terms	**(Attitudes)**	**df**	***F***	***P***
L	Q2.1- Colours/coat patterns	1, 352	26.292	**0.00**
	Q2.2- Hunting skills	1, 352	1.433	0.232
	Q2.3- Size	1, 352	9.877	**0.002**
	Q2.4- Unique feline/cat behaviours	1, 352	10.587	**0.001**
	Q2.5- Worship some/all big cats as deity	1, 352	5.302	0.022
	Q2.6- Roar/Purr	1, 352	9.232	**0.003**
	Q2.7- Cubs	1, 352	3.086	0.08
	Q2.8- Whole animal	1, 352	0.834	0.362
A	Q2.1- Colours/coat patterns	4, 352	0.335	0.854
	Q2.2- Hunting skills	4, 352	1.09	0.361
	Q2.3- Size	4, 352	0.546	0.702
	Q2.4- Unique feline/cat behaviours	4, 352	1.114	0.35
	Q2.5- Worship some/all big cats as deity	4, 352	1.841	0.12
	Q2.6- Roar/Purr	4, 352	0.35	0.844
	Q2.7- Cubs	4, 352	1.023	0.395
	Q2.8- Whole animal	4, 352	2.34	0.055
G	Q2.1- Colours/coat patterns	1, 352	2.129	0.145
	Q2.2- Hunting skills	1, 352	0.749	0.387
	Q2.3- Size	1, 352	1.952	0.163
	Q2.4- Unique feline/cat behaviours	1, 352	6.251	**0.013**
	Q2.5- Worship some/all big cats as deity	1, 352	0.213	0.645
	Q2.6- Roar/Purr	1, 352	0.86	0.354
	Q2.7- Cubs	1, 352	0.603	0.438
	Q2.8- Whole animal	1, 352	1.674	0.197
E	Q2.1- Colours/coat patterns	3, 352	0.329	0.804
	Q2.2- Hunting skills	3, 352	1.073	0.36
	Q2.3- Size	3, 352	1.202	0.309
	Q2.4- Unique feline/cat behaviours	3, 352	0.208	0.891
	Q2.5- Worship some/all big cats as deity	3, 352	1.028	0.38
	Q2.6- Roar/Purr	3, 352	0.092	0.964
	Q2.7- Cubs	3, 352	1.602	0.189

	Q2.8- Whole animal	3, 352	0.205	0.893
Z	Q2.1- Colours/coat patterns	2, 352	3.989	**0.019**
	Q2.2- Hunting skills	2, 352	6.64	**0.001**
	Q2.3- Size	2, 352	1.935	0.146
	Q2.4- Unique feline/cat behaviours	2, 352	5.169	**0.006**
	Q2.5- Worship some/all big cats as deity	2, 352	0.504	0.605
	Q2.6- Roar/Purr	2, 352	0.087	0.916
	Q2.7- Cubs	2, 352	1.319	0.269
	Q2.8- Whole animal	2, 352	4.558	**0.011**
G X E	Q2.1- Colours/coat patterns	3, 352	0.771	0.511
	Q2.2- Hunting skills	3, 352	0.392	0.759
	Q2.3- Size	3, 352	2.492	0.06
	Q2.4- Unique feline/cat behaviours	3, 352	2.71	**0.045**
	Q2.5- Worship some/all big cats as deity	3, 352	0.79	0.5
	Q2.6- Roar/Purr	3, 352	0.312	0.817
	Q2.7- Cubs	3, 352	1.014	0.387
	Q2.8- Whole animal	3, 352	4.163	**0.006**
A X Z	Q2.1- Colours/coat patterns	8, 352	1.742	0.088
	Q2.2- Hunting skills	8, 352	3.357	**0.001**
	Q2.3- Size	8, 352	0.881	0.533
	Q2.4- Unique feline/cat behaviours	8, 352	2.137	**0.032**
	Q2.5- Worship some/all big cats as deity	8, 352	0.66	0.727
	Q2.6- Roar/Purr	8, 352	0.359	0.941
	Q2.7- Cubs	8, 352	2.024	**0.043**
	Q2.8- Whole animal	8, 352	1.064	0.388

'X' represents an interaction between independent variables. Boldface represents a significant difference (P = <0.05)

Table S5. 4 Univariate ANOVAs were used to determine how each subscale contributed to the overall construct – Encounters with big cats

Model terms	Univariate ANOVAs (Attitudes)	df	*F*	*P*
L	Q3.1- Visitors allowed to walk with big cats	1, 332	0.001	0.974
	Q3.2- Visitors feeding big cats	1, 332	4.617	**0.032**
	Q3.3- Visitors posing with big cats or their cubs	1, 332	1.021	0.313
	Q3.4- Visitors allowed to play with big cats or their cubs	1, 332	4.762	**0.03**
	Q3.5- Visitors allowed behind the scenes for a closer look of big cats	1, 332	6.522	**0.011**
	Q3.6- Selfies with big cats	1, 332	0.006	0.94
	Q3.7- Using safari buses for visitors to view big cats in safari parks, large zoo enclosures	1, 332	1.012	0.315
	Q3.8- Live video streaming of big cats in zoos, rescue centres	1, 332	12.137	**0.001**
A	Q3.1- Visitors allowed to walk with big cats	4, 332	3.534	**0.008**
	Q3.2- Visitors feeding big cats	4, 332	2.11	**0.079**
	Q3.3- Visitors posing with big cats or their cubs	4, 332	2.545	**0.04**
	Q3.4- Visitors allowed to play with big cats or their cubs	4, 332	1.91	0.108
	Q3.5- Visitors allowed behind the scenes for a closer look of big cats	4, 332	1.166	0.326
	Q3.6- Selfies with big cats	4, 332	1.681	0.154
	Q3.7- Using safari buses for visitors to view big cats in safari parks, large zoo enclosures	4, 332	0.81	0.52
	Q3.8- Live video streaming of big cats in zoos, rescue centres	4, 332	1.444	0.219
G	Q3.1- Visitors allowed to walk with big cats	1, 332	0.52	0.471
	Q3.2- Visitors feeding big cats	1, 332	0.4	0.527
	Q3.3- Visitors posing with big cats or their cubs	1, 332	0.171	0.679
	Q3.4- Visitors allowed to play with big cats or their cubs	1, 332	0.00	0.994

	Q3.5- Visitors allowed behind the scenes for a closer look of big cats	1, 332	0.013	0.911
	Q3.6- Selfies with big cats	1, 332	0.206	0.65
	Q3.7- Using safari buses for visitors to view big cats in safari parks, large zoo enclosures	1, 332	0.463	0.497
	Q3.8- Live video streaming of big cats in zoos, rescue centres	1, 332	0.036	0.849
E	Q3.1- Visitors allowed to walk with big cats	3, 332	3.606	**0.014**
	Q3.2- Visitors feeding big cats	3, 332	1.359	0.255
	Q3.3- Visitors posing with big cats or their cubs	3, 332	3.343	**0.019**
	Q3.4- Visitors allowed to play with big cats or their cubs	3, 332	3.194	**0.024**
	Q3.5- Visitors allowed behind the scenes for a closer look of big cats	3, 332	1.154	0.327
	Q3.6- Selfies with big cats	3, 332	3.817	**0.01**
	Q3.7- Using safari buses for visitors to view big cats in safari parks, large zoo enclosures	3, 332	0.104	0.958
	Q3.8- Live video streaming of big cats in zoos, rescue centres	3, 332	0.973	0.406
Z	Q3.1- Visitors allowed to walk with big cats	2, 332	0.212	0.809
	Q3.2- Visitors feeding big cats	2, 332	2.097	0.124
	Q3.3- Visitors posing with big cats or their cubs	2, 332	0.38	0.684
	Q3.4- Visitors allowed to play with big cats or their cubs	2, 332	1.291	0.277
	Q3.5- Visitors allowed behind the scenes for a closer look of big cats	2, 332	3.614	**0.028**
	Q3.6- Selfies with big cats	2, 332	0.021	0.979
	Q3.7- Using safari buses for visitors to view big cats in safari parks, large zoo enclosures	2, 332	4.19	**0.016**
	Q3.8- Live video streaming of big cats in zoos, rescue centres	2, 332	7.563	**0.001**
A X G X E	Q3.1- Visitors allowed to walk with big cats	31, 332	1.556	**0.033**
	Q3.2- Visitors feeding big cats	31, 332	1.222	0.199
	Q3.3- Visitors posing with big cats or their cubs	31, 332	1.602	**0.025**
	Q3.4- Visitors allowed to play with big cats or their cubs	31, 332	1.449	0.062
	Q3.5- Visitors allowed behind the scenes for a closer look of big cats	31, 332	1.146	0.276

Q3.6- Selfies with big cats	31, 332	1.919	**0.003**
Q3.7- Using safari buses for visitors to view big cats in safari parks, large zoo enclosures	31, 332	0.863	0.68
Q3.8- Live video streaming of big cats in zoos, rescue centres	31, 332	0.962	0.528

'X' represents an interaction between independent variables. Boldface represents a significant difference (P = <0.05)

Table S5. 5 Univariate ANOVAs were used to determine how each subscale contributed to the overall construct - Environmental conditions preferred for big cats

Model terms	Univariate ANOVAs (Attitudes)	df	*F*	*P*
L	Q4.1- Prefer large green spaces with trees and grass for big cats	1, 334	0.201	0.654
	Q4.2- Prefer enrichment items (such as boxes, toys, ropes, scents etc.) in the enclosure for the cats	1, 334	16.342	**0.00**
	Q4.3- Prefer social animals kept in social groups (such as lions in a pride) and solitary animals (such as tigers) alone	1, 334	41.426	**0.00**
	Q4.4- Hiding spots for big cats to rest and have privacy (which may not be visible to visitors)	1, 334	5.785	**0.017**
	Q4.5- Enough space between different cat enclosures	1, 334	7.509	**0.006**
	Q4.6- Safe and quiet environment	1, 334	0.236	0.628
	Q4.7- Balanced/Controlled visitor numbers	1, 334	0.193	0.661
	Q4.8- Visiting accredited zoos that follow national or state guidelines	1, 334	0.273	0.602
A	Q4.1- Prefer large green spaces with trees and grass for big cats	4, 334	1.097	0.358
	Q4.2- Prefer enrichment items (such as boxes, toys, ropes, scents etc.) in the enclosure for the cats	4, 334	4.117	**0.003**
	Q4.3- Prefer social animals kept in social groups (such as lions in a pride) and solitary animals (such as tigers) alone	4, 334	3.171	**0.014**

	Q4.4- Hiding spots for big cats to rest and have privacy (which may not be visible to visitors)	4, 334	0.786	0.535
	Q4.5- Enough space between different cat enclosures	4, 334	1.066	0.373
	Q4.6- Safe and quiet environment	4, 334	0.92	0.452
	Q4.7- Balanced/Controlled visitor numbers	4, 334	0.376	0.826
	Q4.8- Visiting accredited zoos that follow national or state guidelines	4, 334	1.335	0.257
G	Q4.1- Prefer large green spaces with trees and grass for big cats	1, 334	0.679	0.410
	Q4.2- Prefer enrichment items (such as boxes, toys, ropes, scents etc.) in the enclosure for the cats	1, 334	0.788	0.375
	Q4.3- Prefer social animals kept in social groups (such as lions in a pride) and solitary animals (such as tigers) alone	1, 334	0.424	0.515
	Q4.4- Hiding spots for big cats to rest and have privacy (which may not be visible to visitors)	1, 334	0.023	0.879
	Q4.5- Enough space between different cat enclosures	1, 334	0.172	0.678
	Q4.6- Safe and quiet environment	1, 334	0.317	0.574
	Q4.7- Balanced/Controlled visitor numbers	1, 334	4.328	**0.038**
	Q4.8- Visiting accredited zoos that follow national or state guidelines	1, 334	0.261	0.609
E	Q4.1- Prefer large green spaces with trees and grass for big cats	3, 334	1.066	0.363
	Q4.2- Prefer enrichment items (such as boxes, toys, ropes, scents etc.) in the enclosure for the cats	3, 334	1.532	0.206
	Q4.3- Prefer social animals kept in social groups (such as lions in a pride) and solitary animals (such as tigers) alone	3, 334	2.889	**0.036**
	Q4.4- Hiding spots for big cats to rest and have privacy (which may not be visible to visitors)	3, 334	2.275	0.080
	Q4.5- Enough space between different cat enclosures	3, 334	1.175	0.319
	Q4.6- Safe and quiet environment	3, 334	0.533	0.660

	Q4.7- Balanced/Controlled visitor numbers	3, 334	1.320	0.268
	Q4.8- Visiting accredited zoos that follow national or state guidelines	3, 334	1.027	0.381
Z	Q4.1- Prefer large green spaces with trees and grass for big cats	2, 334	1.523	0.220
	Q4.2- Prefer enrichment items (such as boxes, toys, ropes, scents etc.) in the enclosure for the cats	2, 334	8.646	**0.000**
	Q4.3- Prefer social animals kept in social groups (such as lions in a pride) and solitary animals (such as tigers) alone	2, 334	8.486	**0.000**
	Q4.4- Hiding spots for big cats to rest and have privacy (which may not be visible to visitors)	2, 334	9.536	**0.000**
	Q4.5- Enough space between different cat enclosures	2, 334	3.386	**0.035**
	Q4.6- Safe and quiet environment	2, 334	1.065	0.346
	Q4.7- Balanced/Controlled visitor numbers	2, 334	0.645	0.525
	Q4.8- Visiting accredited zoos that follow national or state guidelines	2, 334	1.991	0.138
L X E	Q4.1- Prefer large green spaces with trees and grass for big cats	3, 334	0.356	0.785
	Q4.2- Prefer enrichment items (such as boxes, toys, ropes, scents etc.) in the enclosure for the cats	3, 334	1.463	0.224
	Q4.3- Prefer social animals kept in social groups (such as lions in a pride) and solitary animals (such as tigers) alone	3, 334	4.144	**0.007**
	Q4.4- Hiding spots for big cats to rest and have privacy (which may not be visible to visitors)	3, 334	1.753	0.156
	Q4.5- Enough space between different cat enclosures	3, 334	2.719	**0.045**
	Q4.6- Safe and quiet environment	3, 334	0.728	0.536
	Q4.7- Balanced/Controlled visitor numbers	3, 334	0.527	0.664
	Q4.8- Visiting accredited zoos that follow national or state guidelines	3, 334	2.157	0.093
A X G	Q4.1- Prefer large green spaces with trees and grass for big cats	4, 334	1.219	0.303

	Q4.2- Prefer enrichment items (such as boxes, toys, ropes, scents etc.) in the enclosure for the cats	4, 334	1.263	0.284
	Q4.3- Prefer social animals kept in social groups (such as lions in a pride) and solitary animals (such as tigers) alone	4, 334	0.984	0.416
	Q4.4- Hiding spots for big cats to rest and have privacy (which may not be visible to visitors)	4, 334	1.873	0.115
	Q4.5- Enough space between different cat enclosures	4, 334	0.939	0.442
	Q4.6- Safe and quiet environment	4, 334	1.543	0.189
	Q4.7- Balanced/Controlled visitor numbers	4, 334	1.456	0.215
	Q4.8- Visiting accredited zoos that follow national or state guidelines	4, 334	1.606	0.172
A X Z	Q4.1- Prefer large green spaces with trees and grass for big cats	8, 334	1.14	0.336
	Q4.2- Prefer enrichment items (such as boxes, toys, ropes, scents etc.) in the enclosure for the cats	8, 334	1.711	0.095
	Q4.3- Prefer social animals kept in social groups (such as lions in a pride) and solitary animals (such as tigers) alone	8, 334	0.995	0.439
	Q4.4- Hiding spots for big cats to rest and have privacy (which may not be visible to visitors)	8, 334	2.392	**0.016**
	Q4.5- Enough space between different cat enclosures	8, 334	1.869	0.064
	Q4.6- Safe and quiet environment	8, 334	1.593	0.126
	Q4.7- Balanced/Controlled visitor numbers	8, 334	1.58	0.13
	Q4.8- Visiting accredited zoos that follow national or state guidelines	8, 334	1.91	0.058
L X E X Z	Q4.1- Prefer large green spaces with trees and grass for big cats	14, 334	0.908	0.55
	Q4.2- Prefer enrichment items (such as boxes, toys, ropes, scents etc.) in the enclosure for the cats	14, 334	1.643	0.066
	Q4.3- Prefer social animals kept in social groups (such as lions in a pride) and solitary animals (such as tigers) alone	14, 334	1.72	**0.050**

	Q4.4- Hiding spots for big cats to rest and have privacy (which may not be visible to visitors)	14, 334	2.014	**0.016**
	Q4.5- Enough space between different cat enclosures	14, 334	1.099	0.357
	Q4.6- Safe and quiet environment	14, 334	1.445	0.13
	Q4.7- Balanced/Controlled visitor numbers	14, 334	1.257	0.233
	Q4.8- Visiting accredited zoos that follow national or state guidelines	14, 334	1.037	0.416

'X' represents an interaction between independent variables. Boldface represents a significant difference (P = <0.05)

Table S5. 6 Univariate ANOVAs were used to determine how each subscale contributed to the overall construct – Interactions with big cat management

Model terms	**Univariate ANOVAs (Attitudes)**	**df**	***F***	***P***
L	Q5.1- Attending keeper talks	1, 318	1.136	0.287
	Q5.2- Visit the animal hospital at the zoo if permitted	1, 318	0.002	0.965
	Q5.3- Participating in research/Volunteering opportunities at zoo	1, 318	1.265	0.262
	Q5.4- Talking to keepers about their big cat's well-being	1, 318	1.935	0.165
	Q5.5- Buying gift certificates to adopt rescued/injured big cats	1, 318	0.216	0.643
	Q5.6- Partnering with zoos for CSR (Corporate Social Responsibility) projects	1, 318	7.840	**0.005**
	Q5.7- Undertaking fundraising events for rescued big cats (e.g., bake, art or photograph sale, etc.)	1, 318	16.213	**0.000**
	Q5.8- Donating to zoos' partnerships to support big cats in the wild	1, 318	13.311	**0.000**
A	Q5.1- Attending keeper talks	4, 318	0.461	0.764
	Q5.2- Visit the animal hospital at the zoo if permitted	4, 318	0.342	0.850
	Q5.3- Participating in research/Volunteering opportunities at zoo	4, 318	1.972	0.099
	Q5.4- Talking to keepers about their big cat's well-being	4, 318	1.000	0.408

	Q5.5- Buying gift certificates to adopt rescued/injured big cats	4, 318	2.407	**0.049**
	Q5.6- Partnering with zoos for CSR (Corporate Social Responsibility) projects	4, 318	1.160	0.329
	Q5.7- Undertaking fundraising events for rescued big cats (e.g., bake, art or photograph sale, etc.)	4, 318	2.559	**0.039**
	Q5.8- Donating to zoos' partnerships to support big cats in the wild	4, 318	1.251	0.289
G	Q5.1- Attending keeper talks	1, 318	0.000	0.990
	Q5.2- Visit the animal hospital at the zoo if permitted	1, 318	4.370	**0.037**
	Q5.3- Participating in research/Volunteering opportunities at zoo	1, 318	1.129	0.289
	Q5.4- Talking to keepers about their big cat's well-being	1, 318	0.054	0.816
	Q5.5- Buying gift certificates to adopt rescued/injured big cats	1, 318	2.047	0.154
	Q5.6- Partnering with zoos for CSR (Corporate Social Responsibility) projects	1, 318	0.025	0.874
	Q5.7- Undertaking fundraising events for rescued big cats (e.g., bake, art or photograph sale, etc.)	1, 318	1.436	0.232
	Q5.8- Donating to zoos' partnerships to support big cats in the wild	1, 318	1.361	0.244
E	Q5.1- Attending keeper talks	3, 318	0.749	0.524
	Q5.2- Visit the animal hospital at the zoo if permitted	3, 318	3.466	**0.017**
	Q5.3- Participating in research/Volunteering opportunities at zoo	3, 318	1.621	0.184
	Q5.4- Talking to keepers about their big cat's well-being	3, 318	1.684	0.170
	Q5.5- Buying gift certificates to adopt rescued/injured big cats	3, 318	0.864	0.460
	Q5.6- Partnering with zoos for CSR (Corporate Social Responsibility) projects	3, 318	0.816	0.486
	Q5.7- Undertaking fundraising events for rescued big cats (e.g., bake, art or photograph sale, etc.)	3, 318	0.437	0.726
	Q5.8- Donating to zoos' partnerships to support big cats in the wild	3, 318	1.448	0.229
Z	Q5.1- Attending keeper talks	2, 318	11.205	**0.000**
	Q5.2- Visit the animal hospital at the zoo if permitted	2, 318	7.122	**0.001**
	Q5.3- Participating in research/Volunteering opportunities at zoo	2, 318	10.422	**0.000**

	Q5.4- Talking to keepers about their big cat's well-being	2, 318	7.329	**0.001**
	Q5.5- Buying gift certificates to adopt rescued/injured big cats	2, 318	5.589	**0.004**
	Q5.6- Partnering with zoos for CSR (Corporate Social Responsibility) projects	2, 318	2.061	0.129
	Q5.7- Undertaking fundraising events for rescued big cats (e.g., bake, art or photograph sale, etc.)	2, 318	2.184	0.114
	Q5.8- Donating to zoos' partnerships to support big cats in the wild	2, 318	10.518	**0.000**
A X E	Q5.1- Attending keeper talks	12, 318	1.046	0.406
	Q5.2- Visit the animal hospital at the zoo if permitted	12, 318	1.363	0.182
	Q5.3- Participating in research/Volunteering opportunities at zoo	12, 318	0.613	0.831
	Q5.4- Talking to keepers about their big cat's well-being	12, 318	0.972	0.475
	Q5.5- Buying gift certificates to adopt rescued/injured big cats	12, 318	1.335	0.197
	Q5.6- Partnering with zoos for CSR (Corporate Social Responsibility) projects	12, 318	0.937	0.509
	Q5.7- Undertaking fundraising events for rescued big cats (e.g., bake, art or photograph sale, etc.)	12, 318	1.478	0.131
	Q5.8- Donating to zoos' partnerships to support big cats in the wild	12, 318	1.169	0.304
L X A	Q5.1- Attending keeper talks	4, 318	1.943	0.103
	Q5.2- Visit the animal hospital at the zoo if permitted	4, 318	0.770	0.545
	Q5.3- Participating in research/Volunteering opportunities at zoo	4, 318	0.965	0.427
	Q5.4- Talking to keepers about their big cat's well-being	4, 318	1.115	0.350
	Q5.5- Buying gift certificates to adopt rescued/injured big cats	4, 318	1.720	0.145
	Q5.6- Partnering with zoos for CSR (Corporate Social Responsibility) projects	4, 318	1.628	0.167
	Q5.7- Undertaking fundraising events for rescued big cats (e.g., bake, art or photograph sale, etc.)	4, 318	0.443	0.777
	Q5.8- Donating to zoos' partnerships to support big cats in the wild	4, 318	0.640	0.635
A X G	Q5.1- Attending keeper talks	4, 318	3.090	**0.016**

	Q5.2- Visit the animal hospital at the zoo if permitted	4, 318	1.916	0.108
	Q5.3- Participating in research/Volunteering opportunities at zoo	4, 318	4.048	**0.003**
	Q5.4- Talking to keepers about their big cat's well-being	4, 318	1.378	0.241
	Q5.5- Buying gift certificates to adopt rescued/injured big cats	4, 318	3.607	**0.007**
	Q5.6- Partnering with zoos for CSR (Corporate Social Responsibility) projects	4, 318	2.868	**0.023**
	Q5.7- Undertaking fundraising events for rescued big cats (e.g., bake, art or photograph sale, etc.)	4, 318	4.049	**0.003**
	Q5.8- Donating to zoos' partnerships to support big cats in the wild	4, 318	4.586	**0.001**
G X Z	Q5.1- Attending keeper talks	2, 318	0.340	0.712
	Q5.2- Visit the animal hospital at the zoo if permitted	2, 318	1.951	0.144
	Q5.3- Participating in research/Volunteering opportunities at zoo	2, 318	2.507	0.083
	Q5.4- Talking to keepers about their big cat's well-being	2, 318	5.445	**0.005**
	Q5.5- Buying gift certificates to adopt rescued/injured big cats	2, 318	0.964	0.383
	Q5.6- Partnering with zoos for CSR (Corporate Social Responsibility) projects	2, 318	0.518	0.596
	Q5.7- Undertaking fundraising events for rescued big cats (e.g., bake, art or photograph sale, etc.)	2, 318	1.498	0.225
	Q5.8- Donating to zoos' partnerships to support big cats in the wild	2, 318	6.979	**0.001**
A X Z	Q5.1- Attending keeper talks	8, 318	0.958	0.469
	Q5.2- Visit the animal hospital at the zoo if permitted	8, 318	1.676	0.103
	Q5.3- Participating in research/Volunteering opportunities at zoo	8, 318	1.397	0.197
	Q5.4- Talking to keepers about their big cats' well-being	8, 318	2.198	**0.027**
	Q5.5- Buying gift certificates to adopt rescued/injured big cats	8, 318	1.390	0.200
	Q5.6- Partnering with zoos for CSR (Corporate Social Responsibility) projects	8, 318	1.320	0.232
	Q5.7- Undertaking fundraising events for rescued big cats (e.g., bake, art, or photograph sale, etc.)	8, 318	2.229	**0.025**

	Q5.8- Donating to zoos' partnerships to support big cats in the wild	8, 318	3.213	**0.002**
A X G X E	Q5.1- Attending keeper talks	15, 318	0.890	0.576
	Q5.2- Visit the animal hospital at the zoo if permitted	15, 318	1.525	0.095
	Q5.3- Participating in research/Volunteering opportunities at zoo	15, 318	1.543	0.088
	Q5.4- Talking to keepers about their big cats' well-being	15, 318	0.827	0.647
	Q5.5- Buying gift certificates to adopt rescued/injured big cats	15, 318	2.051	**0.012**
	Q5.6- Partnering with zoos for CSR (Corporate Social Responsibility) projects	15, 318	0.805	0.672
	Q5.7- Undertaking fundraising events for rescued big cats (e.g., bake, art, or photograph sale, etc.)	15, 318	1.248	0.234
	Q5.8- Donating to zoos' partnerships to support big cats in the wild	15, 318	0.974	0.483

'X' represents an interaction between independent variables. Boldface represents a significant difference (P = <0.05)

Table S5. 7 Univariate ANOVAs were used to determine how each subscale contributed to the overall construct – Big cat welfare concerns

Model terms	**Univariate ANOVAs (Attitudes)**	**df**	***F***	***P***
L	Q6.1- Feeding live prey to big cats (such as live deer, pig, etc.)	1, 361	7.679	**0.006**
	Q6.2- Breeding of big cats should only be for reintroduction to the wild and not for zoos and private owners	1, 361	28.832	**0.000**
	Q6.3- Boredom affects big cats	1, 361	3.422	0.065
	Q6.4- White tigers, white lions & black leopards can be a result of selective breeding in zoos, which may be aimed at obtaining specific coat colours. These coat colours rarely occur naturally. Do you think selective breeding in this way affects big cat conservation	1, 361	1.176	0.279

	Q6.5- Killing of big cats involved in negative incidents/encounters/attacks	1, 361	1.137	0.287
	Q6.6- Private ownership of big cats	1, 361	0.200	0.655
	Q6.7- It is okay to have old or injured big cats (e.g., missing a limb) in zoos	1, 361	7.326	**0.007**
	Q6.8- Big cats should only be bred in their native country for the purpose of conservation	1, 361	27.084	**0.000**
A	Q6.1- Feeding live prey to big cats (such as live deer, pig, etc.)	4, 361	3.146	**0.015**
	Q6.2- Breeding of big cats should only be for reintroduction to the wild and not for zoos and private owners	4, 361	1.612	0.171
	Q6.3- Boredom affects big cats	4, 361	1.274	0.28
	Q6.4- White tigers, white lions & black leopards can be a result of selective breeding in zoos, which may be aimed at obtaining specific coat colours. These coat colours rarely occur naturally. Do you think selective breeding in this way affects big cat conservation	4, 361	0.494	0.74
	Q6.5- Killing of big cats involved in negative incidents/encounters/attacks	4, 361	1.033	0.39
	Q6.6- Private ownership of big cats	4, 361	2.939	**0.021**
	Q6.7- It is okay to have old or injured big cats (e.g., missing a limb) in zoos	4, 361	2.276	0.061
	Q6.8- Big cats should only be bred in their native country for the purpose of conservation	4, 361	0.302	0.876
	Q6.1- Feeding live prey to big cats (such as live deer, pig, etc.)	1, 361	1.855	0.174
	Q6.2- Breeding of big cats should only be for reintroduction to the wild and not for zoos and private owners	1, 361	1.509	0.22
	Q6.3- Boredom affects big cats	1, 361	0.19	0.663
G	Q6.4- White tigers, white lions & black leopards can be a result of selective breeding in zoos, which may be aimed at obtaining specific coat colours. These coat colours rarely occur naturally. Do you think selective breeding in this way affects big cat conservation	1, 361	4.298	**0.039**
	Q6.5- Killing of big cats involved in negative incidents/encounters/attacks	1, 361	6.19	**0.013**
	Q6.6- Private ownership of big cats	1, 361	2.843	0.093

	Q6.7- It is okay to have old or injured big cats (e.g., missing a limb) in zoos	1, 361	4.13	**0.043**
	Q6.8- Big cats should only be bred in their native country for the purpose of conservation	1, 361	1.664	0.198
E	Q6.1- Feeding live prey to big cats (such as live deer, pig, etc.)	3, 361	1.098	0.35
	Q6.2- Breeding of big cats should only be for reintroduction to the wild and not for zoos and private owners	3, 361	1.917	0.126
	Q6.3- Boredom affects big cats	3, 361	0.306	0.821
	Q6.4- White tigers, white lions & black leopards can be a result of selective breeding in zoos, which may be aimed at obtaining specific coat colours. These coat colours rarely occur naturally. Do you think selective breeding in this way affects big cat conservation	3, 361	0.081	0.97
	Q6.5- Killing of big cats involved in negative incidents/encounters/attacks	3, 361	1.506	0.213
	Q6.6- Private ownership of big cats	3, 361	1.664	0.174
	Q6.7- It is okay to have old or injured big cats (e.g., missing a limb) in zoos	3, 361	0.62	0.602
	Q6.8- Big cats should only be bred in their native country for the purpose of conservation	3, 361	0.987	0.399
Z	Q6.1- Feeding live prey to big cats (such as live deer, pig, etc.)	2, 361	0.483	0.617
	Q6.2- Breeding of big cats should only be for reintroduction to the wild and not for zoos and private owners	2, 361	6.334	**0.002**
	Q6.3- Boredom affects big cats	2, 361	4.57	**0.011**
	Q6.4- White tigers, white lions & black leopards can be a result of selective breeding in zoos, which may be aimed at obtaining specific coat colours. These coat colours rarely occur naturally. Do you think selective breeding in this way affects big cat conservation	2, 361	0.059	0.943
	Q6.5- Killing of big cats involved in negative incidents/encounters/attacks	2, 361	3.156	**0.044**
	Q6.6- Private ownership of big cats	2, 361	2.097	0.124
	Q6.7- It is okay to have old or injured big cats (e.g., missing a limb) in zoos	2, 361	9.369	**0.000**

	Q6.8- Big cats should only be bred in their native country for the purpose of conservation	2, 361	4.363	**0.013**
L X Z	Q6.1- Feeding live prey to big cats (such as live deer, pig, etc.)	2, 361	3.696	**0.026**
	Q6.2- Breeding of big cats should only be for reintroduction to the wild and not for zoos and private owners	2, 361	3.709	**0.025**
	Q6.3- Boredom affects big cats	2, 361	1.131	0.324
	Q6.4- White tigers, white lions & black leopards can be a result of selective breeding in zoos, which may be aimed at obtaining specific coat colours. These coat colours rarely occur naturally. Do you think selective breeding in this way affects big cat conservation	2, 361	1.727	0.179
	Q6.5- Killing of big cats involved in negative incidents/encounters/attacks	2, 361	6.739	**0.001**
	Q6.6- Private ownership of big cats	2, 361	1.523	0.219
	Q6.7- It is okay to have old or injured big cats (e.g., missing a limb) in zoos	2, 361	0.457	0.634
	Q6.8- Big cats should only be bred in their native country for the purpose of conservation	2, 361	3.921	**0.021**

'X' represents an interaction between independent variables. Boldface represents a significant difference (P = <0.05)

Appendix E – Chapter 6 Supplementary material

Table S6. 1 Significant events in the history of Sanjay Gandhi National Park related to human-leopard interactions

Year	Significant events in SGNP, its leopards and citizens	Reference
1st Century B.C. - 9th Century A.D.	Formation of *Kanheri* caves	(Joshi, 2013); Pandit (2010)
1847	Formation of the Forest department in India, the appointment of Dr Gibson as Conservator of Forests in Bombay Presidency	Troup (1917)
1875-1881	Records of leopard-human fatalities recorded in the *Dekhan* (Deccan) region and confusion between leopard/pard/panther	Balfour (1885)
1871	Ecology and habits of leopards such as climbing trees, and crossing streams, with emphasis on the Deccan region	McMaster (1871)
1878	Indian Forest Act VII classifies forests into three kinds - reserved forest, protected forest, village forest	Troup (1917)
1885	Indigenous forest tribes of Bombay Presidency include *Chodra, Dhodia, Gamtha, Naikada, Bhil, Kathodi,* ***Thakur, Warli***	Balfour (1885)
1888-1991	Leopard distribution (all over India except parts of Sindh and Punjab) and habits (often found in neighbouring villages, hiding during the day among crops, carrying off sheep, goats and especially dogs at night, found in caves and under piles of rocks, swims well, killed 200 humans in Seoni, MP) recorded	Blanford (1888), Prater (1948)
1890	Forest demarcation and appointment of special Forest Settlement Officers in the Thana collectorate of Bombay Presidency	Bombay Forest Department (1890)
1891	Bombay Forest Department proposal	
1901	Thana collectorate was further divided into Central divisions which consisted of Bombay city, Thana and others	Bombay Forest Department (1901)
1927	The Indian Forest Act 1927 applied to the territories including Bombay and others by consolidating the law relating to forests, the transit of forest produce and the duty leviable on timber and other forest produce.	The Indian Forest Act (1927)
1942	The Bombay Municipal Corporation acquired the catchment areas of two lakes and added the land from the government dairy of Aarey to protect it	Maharashtra Forest Department Records (MFDR)

1950	The Bombay National Parks Act and the formation of Krishnagiri National Park (former name for SGNP) with an area of 19.2 sq. km.	Santapau and Randeria (1955), Bapat (2005)
1952	National Forest Policy was announced in a post-British era	National Forest Policy (1952)
1969	Areas of different ownership of the park were transferred to the Forest Department	Zérah (2007)
1970	A handful of leopards were reported in the park	(Athreya et al., 2007) through JC Daniel (personal communication)
1972	The Wildlife Protection Act was enacted	The Wildlife (Protection) Act (1972)
1972	Distribution of leopards in Peninsular India, clarifying no difference between panther and leopard, along with melanistic leopard mentions from Taroba (Tadoba) Maharashtra	Krishnan (1972)
1975	The Maharashtra Private Forests (Acquisition) Act	Maharashtra Act no. XXIV (1975)
1976	Maharashtra State Revenue and Forest Dept. rename Krishnagiri National Park to Borivali National Park, covering 68.977 sq. km.	Maharashtra State Revenue and Forest Dept. Notification (as cited in Yazdani et al., 1992), Editor-Director (2006)
1977	Management of the National Park gets transferred to the Maharashtra State Forest Development Corporation	MFDR
1980	The Forest (Conservation) Act was enacted	The Forest (Conservation) Act (1980)
1981	The Borivali National Park gets renamed Sanjay Gandhi National Park	Bapat (2005), Rodary, Bruno-Lézy, Landy, Morokawa, and Swanepoel (2018)
1983	The State Govt. adds 19.988 sq. km. to the existing 68.977 sq. km. making the total area 88.965 sq. km. An area of 10.38 sq. km. is set aside as a buffer zone	
1986	Leopard attacks reported for SGNP	MFDR, Edgaonkar and Chellam (1998), Athreya et al. (2007)
1988 (1st April)	The management of SGNP transferred back to the Forest Dept.	MFDR
1988	35 leopards live in SGNP	Athreya et al. (2007), Maharashtra Forest Department Records (MFDR)
1991	The Wildlife (Protection) Act gets amended after Wildlife (Protection) Act, 1972	The Wildlife (Protection) Amendment Act (1991)

1994	Increased human encroachments recorded in SGNP	Mehta (2013) , Zérah (2007), Econet (1997)
1995	The Maharashtra State Govt. declares SGNP as per the provisions of the Wildlife Protection Act 1972, amended in 1991. with an area of 103.09 sq. km.	(Editor-Director, 2006), Subsequent amendments and change in name: WLP 1094 or 177/F-I, dt. 16.1.1995
1995	Writ filed by the Bombay Environment Action Group for encroachments	Writ Petition, 1995 (Writ Petition No. 305 of 1995 in the High Court of Judicature at Bombay, 236p.)
1996	40 leopards recorded in SGNP	Athreya et al. (2007), MFDR
1997	The largest demolition of settlements inside SGNP due to the HC court order affecting indigenous and non-indigenous settlements	Zérah (2007)
2000	"Adivasis and tribals are 'wedded' to the forest and they preserve, protect and propagate forest" stated by the Court	Writ Petition No. 925 of 2000 in the High Court of Judicature at Bombay. Ordinary Original Civil Jurisdiction. Manik Rama Sapte and others versus the State of Maharashtra, Secretary, Department of Forest and Union of India, Secretary, Department of Forest, Government of India, 9p.
2002- 2003	Highest Relocations of leopards	Athreya et al., 2004, 2007
2003- 2004	The highest leopard attacks resulted in death or injury to people in the vicinity of the park	BNHS 2009; unpublished Forest Department records
2009	A relocated radio-collared leopard named *Ajoba* is monitored for travelling 125 km back to Mumbai by swimming across a 70-meter-wide creek	Odden et al. (2014)
2005-2011	"Forest and Wildlife Conservation Centre" under its City Forest Initiative conducted educational awareness campaigns on Human-Wildlife conflicts, in collaboration with Forest Department (SGNP)	Project Report by Forest and Wildlife Conservation Centre
2005	Trapping and relocation of leopards were stopped	(Athreya, 2006; Athreya et al., 2011)
2007-2011	Leopard attacks reduced	BNHS unpublished report, Krishna Tiwari

2001-2011	Media reports related to leopard conflict were assessed revealing the English media tone became neutral after the attacks stopped	Bhatia et al. (2013)
2011	Forest Department initiated a citizen science initiative - 'Mumbaikars for SGNP'	Ghosal (2018)
2011	Awareness workshops organised by the Forest Department for media professionals	Hathaway et al. (2017)
2011-2012	Forest Department sets up camera traps and documents 21 leopards in SGNP	BNHS report, unpublished, Krishna Tiwari
2012-2018	Leopard attacks reported	MFDR
2013 onwards	SGNP Forest Department regularly organises nature trails inside some regions of the park	MFDR
2018 onwards	No fatal leopard attacks since 2018	MFDR
2019	47 leopards recorded in SGNP	MFDR
2020	3 sq. km. of Aarey colony (eco-sensitive zone) becomes part SGNP bringing it to 106 sq. km.	MFDR

Figure S6. 1 Questionnaire and Interview questions used to survey stakeholders

Questionnaire title: Stakeholder perception towards human-leopard interactions in Mumbai

Introductory Information and Consent

Demographic questions
Postcode, age, gender, education level, occupation

Section 1: Leopard as an animal

1.Leopards belong to cat family & are a larger version of domestic cats
2. Leopards are agile & intelligent
3. Leopards do not live inside the forests, and only eat domestic dogs and pigs
4. Leopards rarely attack humans
5. The house cat is thought to be the leopard's aunty
6. Leopards are not scared of humans

Section 2: Leopard as an issue

1.Just like humans, leopards are adaptable & found in most parts of India
2.Mumbai has not changed its way of living with leopards
3.Leopard numbers depend on the availability of food – deer, pigs, dogs
4.The media reports only negative news about leopards
Leopards can share space with humans peacefully
5. If our surroundings clean and litter free, we will not have much of leopard presence

Section 3: When should a leopard be captured

1. When it is seen outside the forest
2. When it has attacked a deer
3. When it has killed a domestic animal
4. When it has attacked a human

Section 4: When should a leopard be kept in captivity permanently?

1. It was caught after it was seen outside a house/property
2. It had killed a pig outside the park
3. It had attacked a person because the person chased a leopard
4. It had killed a person
5. It was caught in a snare and its leg had to be cut

Section 5: What from the following are the threats to urban leopards in Mumbai?

1. Linear infrastructure
2. Road kills
3. Poaching
4. Decline in prey
5. Dumping of debris
6. Illegal liquor dens
7. People's intolerance to wild animals
8. Bad bureaucratic management
9. Negative reporting by media

Section 6: Mumbai has not recorded any leopard attacks since 2018. What do you think has contributed to this reduction of leopard attacks in Mumbai?

1. Awareness about facts & cautious leopard safety practices
2. There are very few leopards left now in SGNP
3. Formation and active participation of citizen science groups
4. Accurate Media representation
5. Prompt action from Forest Department and other authorities such as police, BMC

Additional questions:

1. Where do you get your current information about leopards and the Sanjay Gandhi National Park?
2. Have you interacted with any of the following groups/people about SGNP leopards?

Interview Questions

Q1 How is your locality/ Forest Department/ Research/ NGO/ CSG group/ media reporting/ volunteering contributing towards protecting SGNP and improving human-animal interactions among the people of Mumbai? Can you share some examples?

_____

Q2 Forest Department officer/Researcher/NGO/CSG/Media reporter/Volunteer: How are people made aware of your work? What mode of communication do you use?

_____

Q3 Forest Department officer/Researcher/NGO/CSG/Media reporter/Volunteer: What challenges do you or your work face with regard to leopards or people around SGNP?

_____

Q4 Forest Department officer/Researcher/NGO/CSG/Media reporter/Volunteer: It seems that Mumbai is setting a good example of human-leopard interactions to the world. Is there anything else you would like to add that has contributed to this?

_____

Table S6. 2 Participants of this study, the nature and level of their activities, and possible influence on human-leopard interactions

Locals (Indigenous/Non-indigenous)		
Stakeholder	*Nature and Level of Activity*	*Possible influence on human-leopard interactions*
1. Yeoor resident	A local living on the east side of SGNP	Living near leopards
2. Indigenous resident	An indigenous local living on the south-west side of the National Park	Indigenous inhabitant belonging to the *Warli* tribe worships the leopard deity - *Waghoba* and lives near leopards
3. SGNP building resident	Local living on the west side of SGNP	Living near leopards
4. Non-indigenous SGNP resident	A local living on the west side of SGNP	Living near leopards
5. Aarey resident	A local living towards the south of SGNP	Living near leopards
Forest Department officials		
Stakeholder	*Nature and Level of Activity*	*Possible influence on human-leopard interactions*
1. Principal Chief Conservator of Forest	The highest-ranking order of the Forest Department	In charge of making management decisions for SGNP
2. RFO SGNP	Range forest officer for SGNP zone	Responsible for the execution of all works in the Range
3. RFO Yeoor	Range forest officer for Yeoor zone of SGNP	Responsible for the execution of all works in the Range
4. Forest Guard, Yeoor	Protection of the park and its animals	Forest guards responsible for on-ground duties of patrolling the park and monitoring the zones
5. Rescue team member Forest Guard	The Forest guard is responsible for on-ground duties of patrolling the park and monitoring the zones, and also gets involved in rescue operations.	
Researcher		
Stakeholder	*Nature and Level of Activity*	*Possible influence on human-leopard interactions*
Researcher 1	Research aimed to contribute to policy, management and conservation of leopards	Involved in the camera trapping project to study leopard movements and conducted research on the indigenous

		inhabitants of SGNP and how they share spaces with the leopards.
Researcher 2	Research aimed to contribute to policy, management and conservation of leopards	The research project focused on collecting baseline data on the ecology, numbers, and food habits of leopards
Researcher 3	Research aimed to contribute to policy, management of SGNP and socio-economic status of locals.	Researcher and Professor working on the invertebrate's biodiversity and supervised students on the social issues projects
Researcher 4	Research aimed to contribute to policy, and management of SGNPs leopards through raising awareness.	Naturalist working with different locals/citizens to raise awareness on issues within the park about biodiversity, with past research on fig trees
Researcher 5	Research aimed to contribute to policy, and management of SGNPs leopards through raising awareness.	As a naturalist, designs citizen science projects to involve nature or wildlife enthusiasts. Also, assists the Forest Department in collecting data such as bird surveys.

Non-Governmental Organisation		
Stakeholder	*Nature and Level of Activity*	*Possible influence on human-leopard interactions*
1. Resqink Association for Wildlife Welfare (RAWW)	RAWW is a registered charitable organisation working in Mumbai for wildlife conservation and human-wildlife conflict mitigation.	RAWW works closely with the Forest Department, assisting them in leopard conflict situations or rescuing wild animals and raising awareness.
2. World Wide Fund for Nature (WWF)	WWF India is a science-based organization which addresses issues such as the conservation of species and their habitats, climate change, water, and environmental education, among many others.	WWF conducts classroom educational programs in government schools and communities, organises nature trails for citizens/students to various parts of SGNP, and raises awareness about leopards and locals.
3. Vanashakti	Vanashakti is a Mumbai based non-profit, non-governmental environmental organization that strives to address issues of environmental conservation at all levels using education, awareness and litigation to achieve its objectives.	Vanashakti pioneered in filing petitions against illegal tree cutting in Aarey and is dedicated to protecting Aarey for the last 7 years. They were instrumental in getting the eco-sensitive zone of SGNP notified legally, filing complaints against encroachers and interacting with the locals to raise awareness about the leopards or garbage issues.

4. Bombay Natural History Society (BNHS)	The Bombay Natural History Society (BNHS), a pan-India wildlife research organization, has been promoting the cause of nature conservation since 1883.	BNHS started a program called 'City Forest', which focused on conservation issues of SGNP and was not limited to educating locals and indigenous living inside the park, but also other stakeholders - media, police officials (e.g., controlling mob in leopard incidences).
5. GreenLine	In 2010, GreenLine was started to address and raise awareness about the environmental issues of Mumbai through three campaigns - Green Schools Campaign, Green Lead Volunteers and Green Lifestyle Initiative	GreenLine was actively involved in the 'Save Aarey' campaign and was among the first petitioners to file PIL against the proposed metro car shed. They were involved in protecting Aarey by creating awareness, going for protests, forming citizen science groups, working with other NGOs and researchers, conducting research and surveys in and around SGNP through their campaigns.

Civil Society Groups

Stakeholder	*Nature and Level of Activity*	*Possible influence on human-leopard interactions*
1. Mumbaikars for SGNP (MfSGNP)	MfSGNP is a citizen-science project that uses basic scientific methods to better understand the beauty, importance and challenges faced by the leopards and the Park, to increase positive action and coexistence between humans and wildlife.	-MfSGNP is directly involved with different stakeholders and have a project called "Living with leopards" where citizens are aware of the mitigation protocol. Activities are organised to make children aware and curious of their surroundings and help build the relationship of man with nature.
2. Aarey Conservation Group (ACG)	Aarey Conservation Group (ACG) is a local group committed to enriching and promoting Aarey as a pristine green zone for Mumbaikars.	-ACG created petitions, campaigns, filing objections to Municipal Council for tree cutting in Aarey. ACG aims to protect Aarey through tree plantation, clean-ups, butterfly garden visits, social media activism, urban-indigenous meetups, indigenous tribal lunches, traditional ecological knowledge such as wild uncultivated food and the leopard deity Waghoba
3. Urban Biodiversity Conservation group (UBCG)	UBCG is a small group organising outdoor activities by meeting in Yeoor and going for nature walks.	-Primary objective of UBCG is to create awareness about the importance of conservation of biodiversity amongst citizens and contribute to conservation in urban areas under the guidance of experts.
4. Morning walkers' group	The morning walkers group occasionally meets for walks in the park	-Walkers advise other visitors not to litter, report forest fires and pick up garbage. They were also involved in the leopard

		research project and helped set up and remove camera traps for researchers.
5. Nature educator at SGNP and MfSGNP	SGNP has independent nature educators and MfSGNP is a citizen science project which acts as a mediator for the Forest Department to address issues where there are interactions between humans and leopards.	-As a nature educator, the participant takes individuals and children on nature trails and talks about issues related to the park and leopards. At MfSGNP, participant conducted workshops on coexistence for media and capacity building across various departments.
Media professional		
Stakeholder	*Nature and Level of Activity*	*Possible influence on human-leopard interactions*
1. Midday newspaper	Newspaper that publishes the local, national and global news	-Through interactions with the FD and researchers, there is a change in reporting stories on leopards. Also report issues faced by the locals around the park such as lack of public amenities -toilets, electricity or water connections that could have led to past conflict
2. DNA/Mumbai Mirror newspaper	Newspaper that publishes the local, national and global news	-Between 2009 & 2015, participant ensured that the news on leopards was not made sensational, but only included facts and real stories. Later joined the organisation Centre for Wildlife Studies to educate other news reporters to publish news that would sensitise
3. Sakal Media	Newspaper that publishes the local news in English and the regional language Marathi	-Participant has been reporting on leopards, locals and the environment in English and *Marathi*. Articles published brought attention and justice to the locals living without basic amenities and were vulnerable to negative incidences.
4. Hindustan Times	Newspaper that publishes the local, national and global news	-Participant's reporting increased awareness to understand what's happening in the national park. By collecting information from the FD as the major source and others, it was translated into stories that got the attention of the readers.
5. Times of India	Newspaper that publishes the local, national, and global news	-Regular reporting on the SGNP has helped raised awareness and pushed for better policies to conserve and protect the park better. Data gathered for an article is mostly from locals,

environmentalists, scientists from various institutes, documents and officials.

Student volunteers		
Stakeholder	*Nature and Level of Activity*	*Possible influence on human-leopard interactions*
1. Wilson College student	Volunteering opportunities within the park	-Volunteered to study human-leopard interactions around Mumbai; to help avoid conflict and make people tolerant of leopard presence
2. KJ Somaiya College student	Volunteering opportunities within the park	-Volunteered to interact with locals to make them aware of leopards
3. St Xavier's College student	Volunteering opportunities within the park	-Volunteered to collect data on diet and abundance of leopards, and further develop strategies to mitigate conflict and raise awareness
4. VIVA College student	Volunteering opportunities within the park	-Volunteering involved talking to people, sharing facts and making them aware of the presence of leopards and have assisted the locals in deploying camera traps
5. Bhavans College student	Volunteering opportunities within the park	-By studying leopard movements, the behaviour and routine of these cats are used to educate/inform locals and share ideas on how to avoid conflicts with the leopards

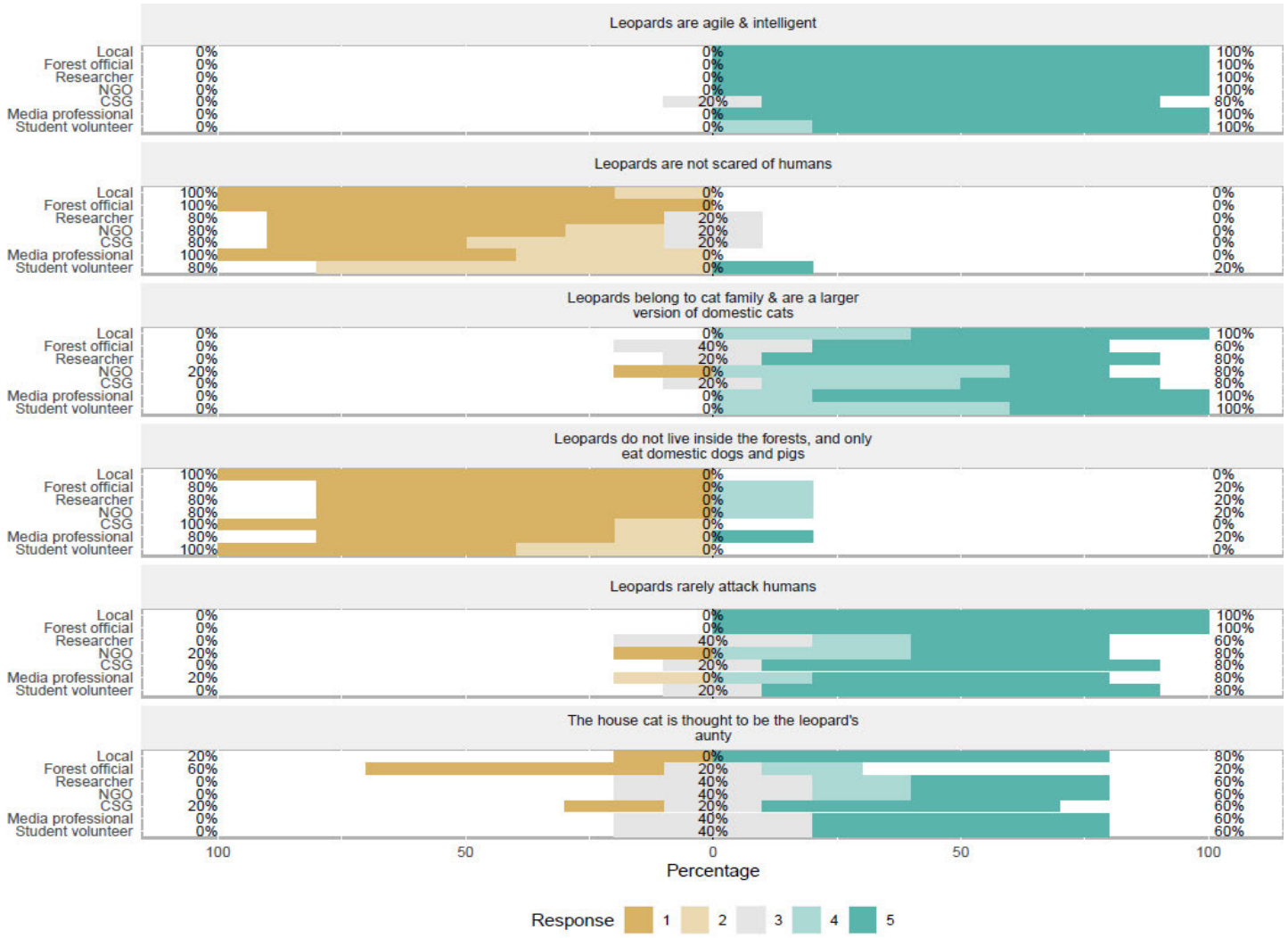

Figure S6. 2 Diverging stacked bar charts showing similarities and differences in stakeholder perceptions of leopards around Sanjay Gandhi National Park (n=35) in a response scale consisting of items of the Likert type (1 = strongly disagree to 5 = strongly agree). The question was: 'What are your perceptions of the leopard as an animal?'

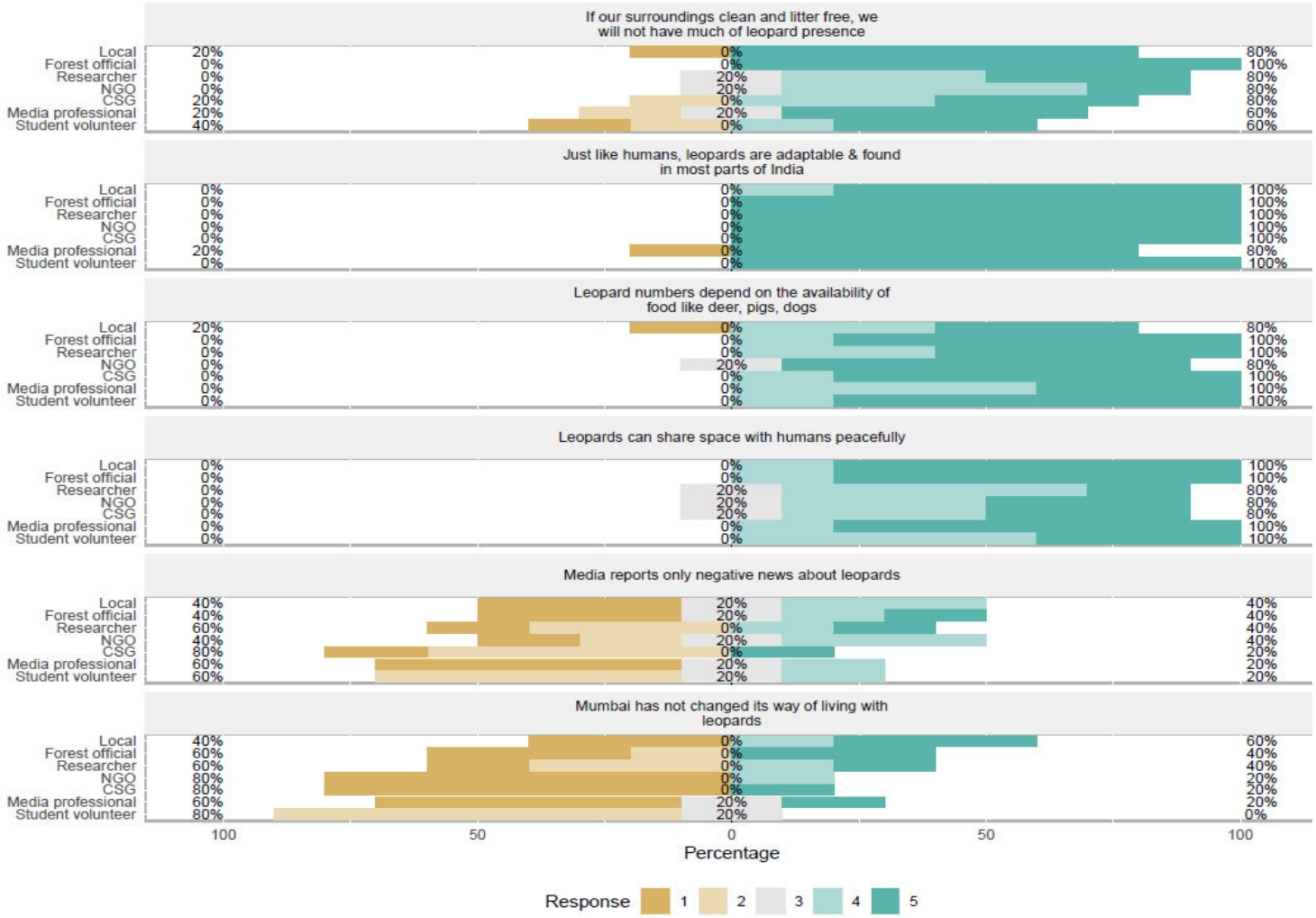

Figure S6. 3 Diverging stacked bar charts showing similarities and differences in stakeholder perceptions of leopards around Sanjay Gandhi National Park (n=35) in a response scale consisting of items of the Likert type (1 = strongly disagree to 5 = strongly agree). The question was: 'What are your perceptions of leopard as an issue?'

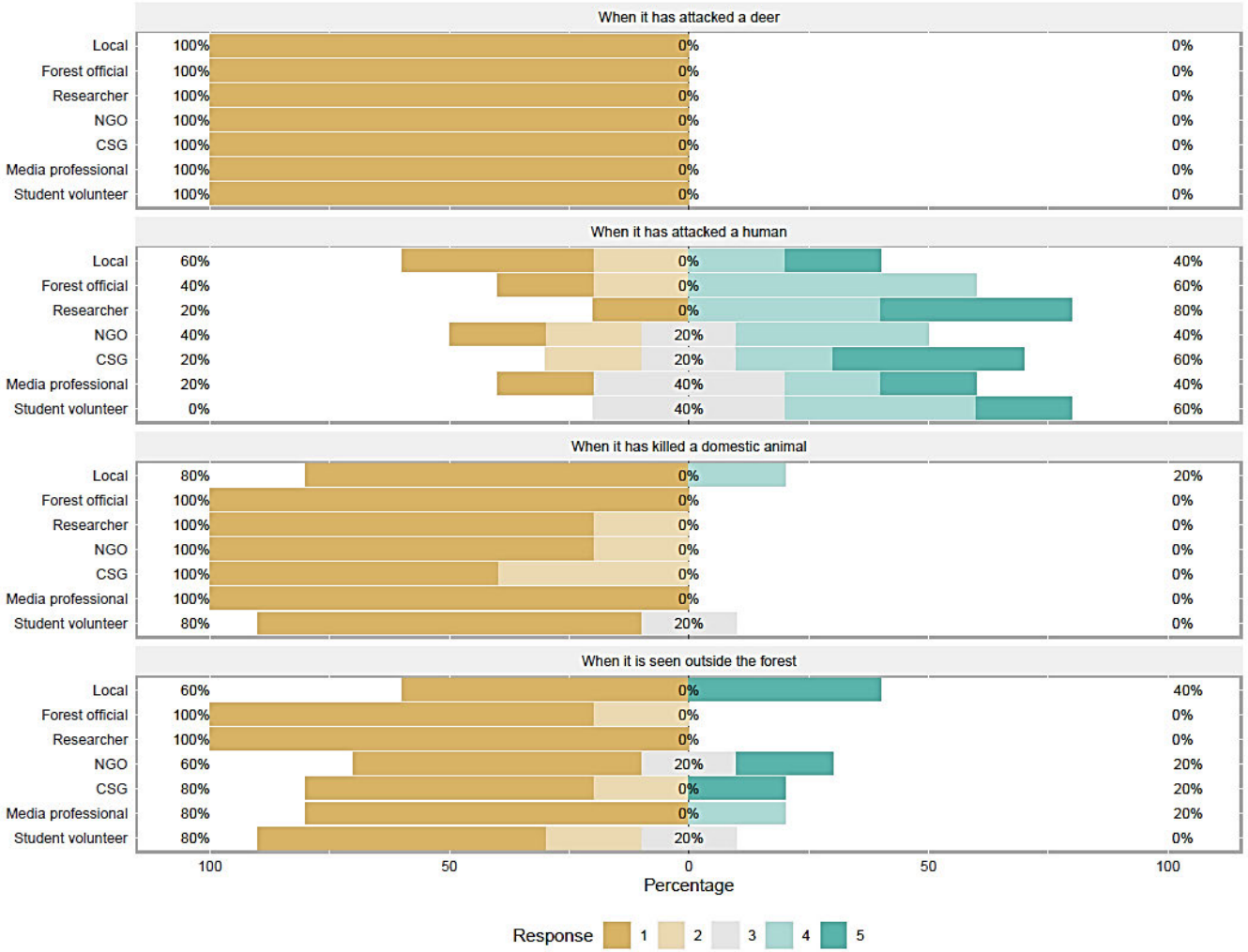

Figure S6. 4 Diverging stacked bar charts showing similarities and differences in stakeholder perceptions of leopards around Sanjay Gandhi National Park (n=35) in a response scale consisting of items of the Likert type (1 = strongly disagree to 5 = strongly agree). The question was: 'When should a leopard be captured'?

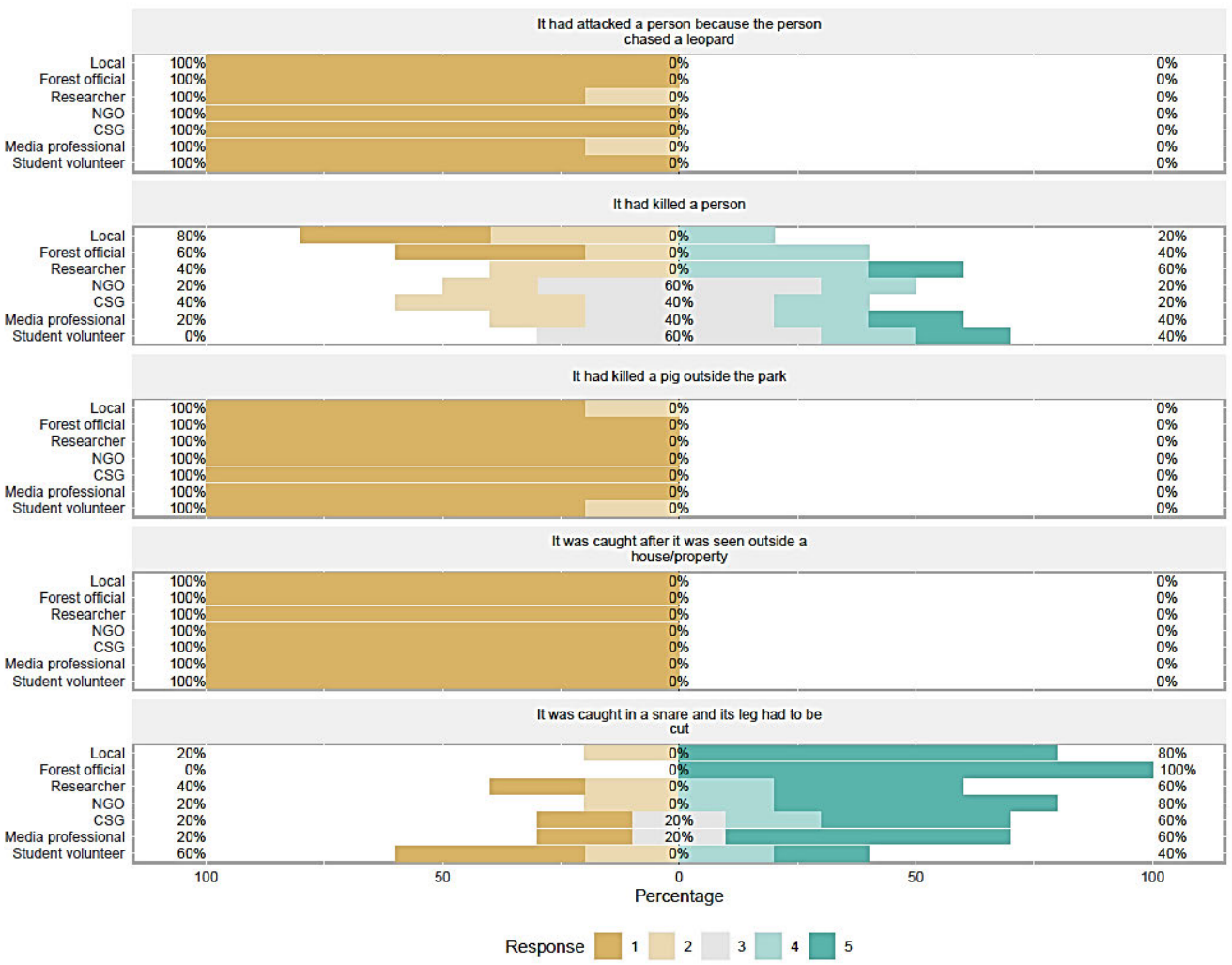

Figure S6. 5 Diverging stacked bar charts showing similarities and differences in stakeholder perceptions of leopards around Sanjay Gandhi National Park (n=35) in a response scale consisting of items of the Likert type (1 = strongly disagree to 5 = strongly agree). The question was: 'When can a leopard be kept in captivity?'

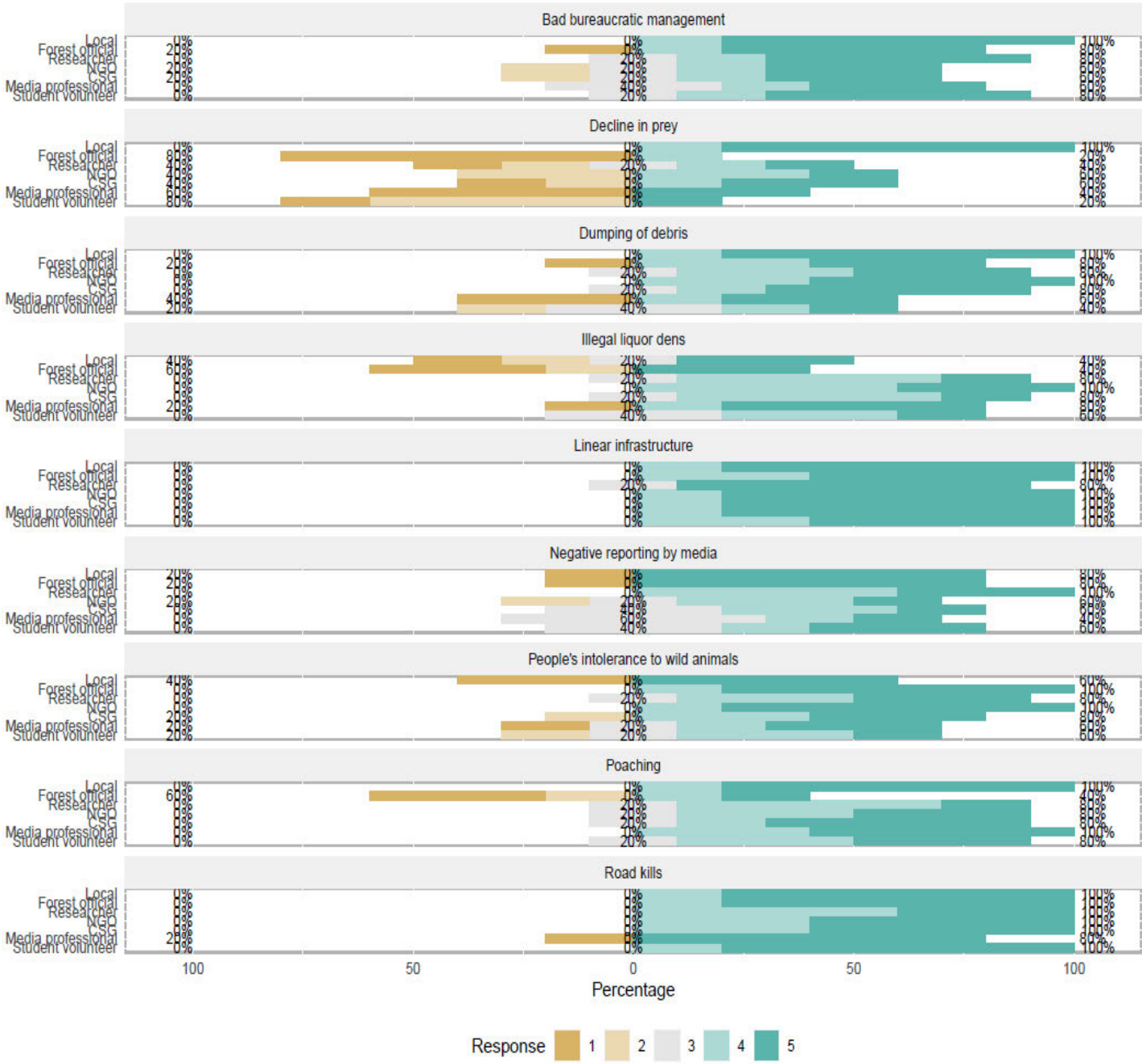

Figure S6. 6 Diverging stacked bar charts showing similarities and differences in stakeholder perceptions of leopards around Sanjay Gandhi National Park (n=35) in a response-scale consisting of items of the Likert type (1 = strongly disagree to 5 = strongly agree). The question was: 'What are the threats faced by the urban leopards of Mumbai'?

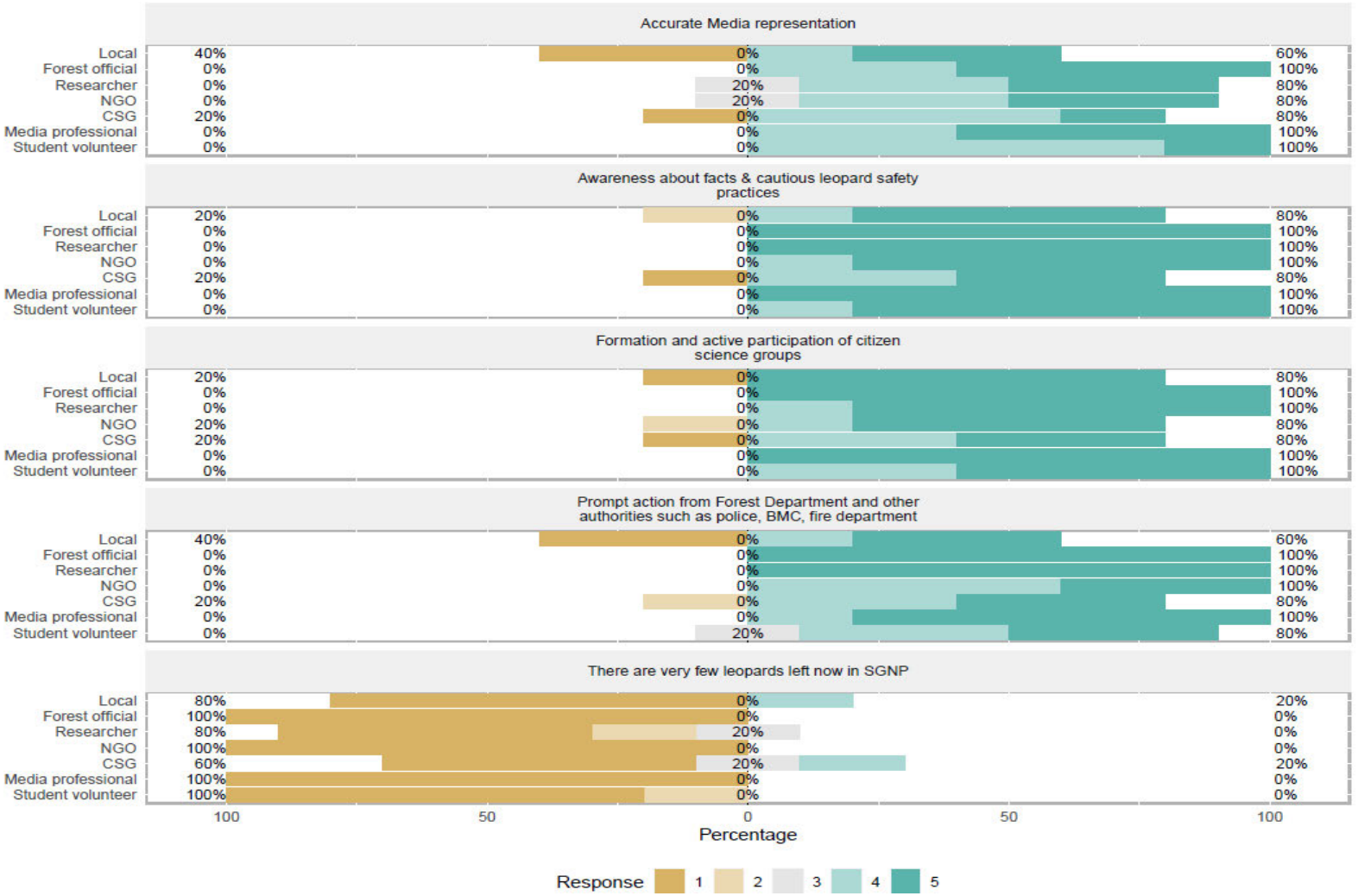

Figure S6. 7 Diverging stacked bar charts showing similarities and differences in stakeholder perceptions of leopards around Sanjay Gandhi National Park (n=35) in a response scale consisting of items of the Likert type (1 = strongly disagree to 5 = strongly agree). The question was: 'What are the factors contributing to the reduction in leopard attacks?'

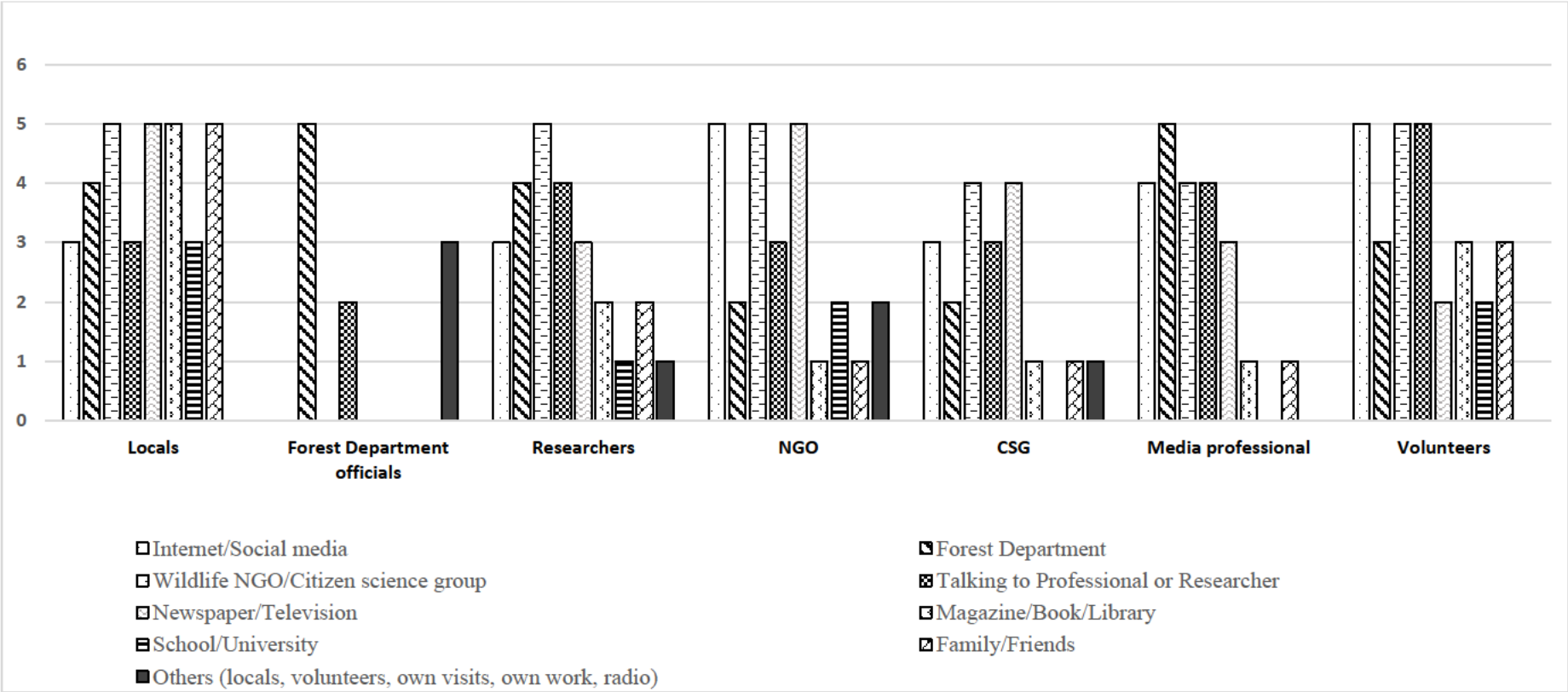

Figure S6. 8 Stakeholder's current sources of knowledge about Mumbai's leopards

Table S6. 3 Summary of the discriminant functions obtained from the discriminant function analysis (DFA) with reverse-scored acceptable, moderate and high-reliability subscales for Q1, Q2, Q4, Q5 and Q6. The analysis yielded six functions explaining 97.6% of the total variation for predicting group membership.

Perceptions	Function					
	1	2	3	4	5	6
Eigenvalue	13.913	8.677	2.865	1.920	1.092	0.712
% Variation	47.7	29.7	9.8	6.6	3.7	2.4
Q6.5 Prompt action from Forest Department and other authorities such as police, BMC	0.056	0.051	**-0.340***	-0.046	-0.204	-0.111
Q5.4 Decline in prey	-0.069	0.012	**0.335***	0.134	-0.116	0.131
Q6.4 Accurate Media representation	0.014	0.022	-0.259*	-0.119	-0.048	0.004
Q6.1 Awareness of facts & cautious leopard safety practices	0.001	0.121	-0.245*	-0.152	-0.027	0.070
Q4.4 It (the leopard) had killed a person	-0.067	0.025	-0.239*	0.110	0.041	-0.209
Q2.3 Leopard numbers depend on the availability of food like deer, pigs, dogs	0.044	-0.048	-0.209*	0.111	0.089	-0.050
Q5.3 Poaching	-0.175	-0.024	0.203*	0.117	-0.091	-0.134
T1.3 Leopards do not live inside the forests, and only eat domestic dogs and pigs	0.013	-0.014	0.143*	0.074	0.117	0.014
Q5.8 Bad bureaucratic management	-0.012	0.074	0.119*	-0.030	0.116	-0.100
Q2.5 Leopards can share space with humans peacefully	0.003	-0.020	0.082	-0.385*	0.054	0.013
Q2.1 Just like humans, leopards are adaptable & found in most parts of India	0.067	0.013	0.016	0.209*	0.177	0.146
Q6.3 Formation and active participation of citizen science groups	0.016	0.076	-0.143	-0.191*	-0.020	-0.128
Q5.6 Illegal liquor dens	-0.073	-0.016	-0.090	0.185*	-0.122	0.042
Q1.5 The house cat is thought to be the leopard's aunty	-0.146	0.024	0.079	0.152*	-0.015	-0.107
Q4.2 It had killed a pig outside the park	-0.036	0.031	0.128	-0.036	**0.307***	-0.021
Q1.4 Leopards rarely attack humans	0.060	-0.036	0.151	-0.160	0.222*	-0.118
Q5.2 Road kills	0.033	-0.006	0.065	0.004	0.207*	0.122
Q2.6 If our surroundings clean and litter free, we will not have much of leopard presence	0.084	0.013	0.019	-0.110	-0.146*	0.070
Q5.1 Linear infrastructure	-0.026	-0.034	0.050	-0.007	-0.089*	0.065
Q5.7 People's intolerance to wild animals	0.075	0.000	-0.127	0.061	-0.110	**0.315***
Q5.5 Dumping of debris	0.025	0.008	0.211	0.182	-0.117	**0.280***
T6.2 There are very few leopards left now in SGNP	-0.017	0.036	-0.173	-0.213	0.041	0.277*
Q4.3 It had attacked a person because the person chased a leopard	-0.031	0.062	-0.081	-0.028	-0.238	-0.265*
Q1.2 Leopards are agile & intelligent	-0.002	0.106	-0.014	-0.153	-0.129	0.186*
Q5.9 Negative reporting by media	0.041	0.058	0.049	0.016	0.055	-0.104*

Discrimination function loadings >.28 are in bold and show pooled within-groups correlations between discriminating variables and standardized canonical discriminant functions. Variables are ordered by the absolute size of correlation within the function. * Largest absolute correlation between each variable and any discriminant function.

References

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