Personality Matters: Exploring the Relationship between Personality and Stress Physiology in Captive African Lions

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

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Abstract

Background: Considering animals as individuals and not as species is becoming increasingly essential to animal welfare management. 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 in isolation. Our research shows how integrating an improved understanding of the personality of big cats with stress physiology may enhance welfare, especially endangered species like African lions. By using a wild cat personality checklist, this study compared African lion personality with its faecal stress glucocorticoids non-invasively.

Results: We identified three personality types for individual African lions (Dominance, Agreeableness and Neuroticism) and examined whether these dimensions varied with stress cortisol levels. When controlling for differences in age across lions, we found a strong negative correlation between Agreeableness in lions and their glucocorticoid levels. This suggests that the personality of a lion may help it cope with its surroundings.

Conclusions: Our findings can assist with the better management of big cats and it is proposed that ex-situ managers of zoos and rescue centres incorporate the personality data of their animals into the Zoological Information Management Software (ZIMS). This data can be accessed globally and can be useful for caretakers managing their animals according to their needs while undergoing veterinary procedures or in reintroduction programs. Thus, by improving individual welfare, we can improve overall welfare of big cats.

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

Background

Improving the individual and overall welfare of big cats is an ongoing concern [1]. 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 [2]. However, 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 [3, 4]. Individual differences, or animal personality, is defined as the set of behaviours exhibited consistently across time and situations [5-7]. One way of understanding a big cat's personality is by observing its behaviour or coping style under a challenging situation (Vaz *et al.*, in press, [6]).

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 [6]. Internally, the animal initiates a neuroendocrine stress response when faced with a stressor, that releases stress hormones called catecholamines (rapid flight-fight response) and glucocorticoids (slow responding endocrine response) with acute or chronic effects [8-10]. However, the way an animal perceives these stressors may vary due to its personality, which is highlighted in its glucocorticoid (GC) levels [11]. 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 stress levels [12].

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 [13]. A variety of behavioural tests and checklists have been developed in the past decade to help identify traits of wellbeing and the personalities among big cats (Vaz *et al.*, in press); these tests and checklists have been used for lions [14-18], tigers [19-21], jaguars [22], cheetahs [23-26], snow leopards [27, 28], and in particular the Asiatic lion personality [15, 17] and African lion personality [14, 16, 18]. Similarly, studies have tried to understand the stress physiology and variation in GCs for lions [29-31]. Predominantly, a large portion of the published literature focuses on understanding either the personality or stress physiology of big cats. This research explores the connections between big cats' personality and individuals' stress physiology to better understand individual animals' adaptive capacity and vulnerability to stressors to promote wellbeing [6].

In humans, exploring human personality has helped psychologists perceive the ways people respond to stressors and thus develop strategies to overcome them. Similarly, understanding the personality of lions can assist caretakers in ensuring the wellbeing of lions by developing suitable approaches before stressful circumstances such as veterinary procedures. 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 [32]. The findings suggest that lions which were more social and less neurotic had lower GCs, indicating that social animals coped better [32]. 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 (Vaz *et al.*, in press, [14]). 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 further understand the relationship between personality and stress.

This study identifies the personality types of African lions and examines if there is a relationship between personality and stress physiology. The study specifically investigates the influence of biological factors such as gender, age, core body temperature, along with the origin and location of the lion. Based on past research [16], we predict males would be more dominant than females. Also, due to separate biological functions between the sexes, 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 [12, 33]. 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 affect its coping style. Accordingly, we first tested if these factors were linked to lion personality alone. The influence of these factors on the lions' stress GC levels was then assessed. It was expected that personality differences would correlate with differences in physiological states, such as GC levels. Lastly, we investigated if any of these nominated factors may impact the integrated relationship of personality and stress physiology.

Results

Personality of African lions

Extracting personality axes

An examination of the total variance from unrotated Principal Component Analysis (PCA) indicated that 9 factors accounted for 87.57% of the variation in lion behaviour. However, parallel analysis indicated that only the eigenvalue of the first three principal components (PC) in the raw dataset exceeded these chance values, suggesting that these factors underlie the personality types (Table S3). Thus, the parallel analysis (Table S3) reduced the 9 components to 3 components explaining 61.96% variation and were labelled as PC1, PC2 and PC3, where a value of 0.5 or above was considered to be biologically important (Table 1).

PC1 had an eigenvalue of 13.76 and explained 31.28% of the cumulative variance in the data representing a Dominance axis. The traits bold, bullying, dominant, aggressive to people, inventive, jealous and tense loaded strongly and positively, while the traits affectionate, gentle, stable, submissive and trusting loaded negatively (Table 1). Hence, lions having higher

PC1 scores were bolder compared to those with lesser scores, indicating more dominant individuals.

PC2 had an eigenvalue of 9.17, which explained 20.85% of the variance in the data representing an Agreeableness axis. The traits of being aggressive to conspecifics, excitable, inquisitive, playful, smart and trusting loaded strongly and positively, while aggressive to people and irritable loaded negatively (Table 1). Hence, animals with higher PC2 scores were more agreeable, and those that scored low were more antagonistic.

PC3 had an eigenvalue of 4.32 and explained 9.82% of the variance in the data representing a Neuroticism axis. The behavioural traits anxious, clumsy, insecure, submissive, and timid loaded positively while traits such as bold and dominant loaded negatively (Table 1). Hence, lions with higher PC3 scores were more neurotic and anti-social than those with lower scores, which were more stable.

Based on the pattern of factor loadings, the three PCs were labelled as Dominance, Agreeableness and Neuroticism, respectively.

Effect of gender, origin, location, age and core body temperature on personality

The Dominance of African lions differed significantly with gender; with males (*Mean* = 0.49, *SD* = 0.84) being significantly more dominant than females (*Mean* = -0.72, *SD* = 0.74) (Table 2). In contrast, male (*Mean* = -0.07, *SD* = 1.04) and female lions (*Mean* = 0.11, *SD* = 0.98) did not differ in their Agreeableness (Table 2). Similarly, there was no significant difference in Neuroticism between males (*Mean* = -0.15, *SD* = 1.09) and females (*Mean* = 0.22, *SD*= 0.84) (Table 2).

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

Personality type	Factors	SS	*df*	*F*	*P*
Dominance	Gender	7.943	1,20	12.162	**0.002**
	Origin	1.515	1,20	1.555	0.227
	Location	2.638	1,20	2.873	0.106
Agreeableness	Gender	0.186	1,20	0.178	0.677
	Origin	1.273	1,20	1.292	0.269
	Location	2.701	1,20	2.954	0.101
Neuroticism	Gender	0.755	1,20	0.747	0.398
	Origin	0.332	1,20	0.321	0.577
	Location	2.119	1,20	2.249	0.149

Origin did not differ significantly for Dominance, Agreeableness or Neuroticism. Similarly, location of the lions did not differ with personality type, with no significant difference found for Dominance, Agreeableness or Neuroticism (Table 2). Simple linear regression showed a significant negative relationship between Dominance and age, with an R^2 of 0.283 indicating that younger individuals were more dominant than older individuals (Table 3). Similarly, there was a significant negative relationship between Agreeableness and age, with an R^2 of 0.213 indicating that Agreeableness declines with age (Fig. 1).

However, there was no significant relationship between Neuroticism and age. Also, no significant relationship was found between core body temperature and Dominance, Agreeableness, or Neuroticism (Table 3).

Table 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

Personality type	Factors	Std Coefficients		*t*	*df*	*F*	*P*
		Beta	Std. Error				
Dominance	Age	-0.597	0.036	-3.324	1,20	11.049	**0.003**
	Core Eye Temperature	0.201	0.253	0.917	1,20	0.841	0.37
Agreeableness	Age	-0.451	0.04	-2.26	1,20	5.107	**0.035**
	Core Eye Temperature	0.235	0.251	1.083	1,20	1.173	0.292
Neuroticism	Age	-0.017	0.045	-0.063	1,20	0.006	0.939
	Core Eye Temperature	0.059	0.258	0.263	1,20	0.069	0.795

Stress Glucocorticoid Hormones

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.

Effect of gender, origin, location, age and core body temperature on stress physiology

The ANOVA showed no significant interaction between cortisol and gender ($F_{(1, 20)} = 2.659$, $P = 0.119$). The cortisol levels of the male African lions (*Mean* = 0.202, *SD* = 0.007) did not differ from those of the females (*Mean* = 0.197, *SD* = 0.007). Similarly, there was no significant interaction between cortisol and 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 interaction between cortisol and location of the lion ($F_{(1, 20)} = 2.092$, $P = 0.164$). 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 body temperature ($R^2 = 0.001$, $F_{(1, 20)} = 0.019$, $P = 0.892$).

Relationship between personality and stress controlling for the effects of age

When controlling for age (9.13 ± 4.95 years), there was a strong negative correlation ($r = -0.467$, $P = 0.029$) found between Agreeableness and cortisol levels. The results show that younger individuals are more agreeable and have lower cortisol levels as compared to older lions. In contrast, there was no significant relationship found for Dominance ($P = 0.316$) and Neuroticism ($P = 0.183$) on controlling age.

Discussion

The present study assessed the links between the personality of African lions with their stress physiology to recognise factors that shape individual welfare. To determine the current coping style of the lions, the personality of each lion was assessed by a rating method and the cortisol levels from fresh faecal samples [14, 30]. The literature shows that there are many factors that may influence either the personality or stress physiology of big cats. Our study quantifies the effects of factors such as gender, age, core body 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 that the relationship of personality and stress is influenced by age, where older lions are less agreeable with higher levels of cortisol than younger lions. The behavioural traits in the younger agreeable lions, such as being excitable, friendly to people, inquisitive, playful, and aggressive to conspecifics may help them to cope with a challenging situation.

Personality of lions at Zambi Wildlife Retreat and Sydney Zoo

The lions at both study sites were reliably rated by the keepers and the researcher. These ratings were dependent on either experience with the animals or on existing knowledge of feline behaviours [17]. From the reliably rated factors, the African lions fit under the three main personality dimensions of Dominance, Agreeableness and Neuroticism, similar to previous findings for various wild cats [14, 32, 34]. Dominance loaded positively and strongly for behavioural traits - bold, bullying, dominant, aggressive to people, inventive, jealous and tense, while the behavioural traits affectionate, gentle, stable, submissive and trusting loaded negatively. Previous studies rated reintroduced African lions for their boldness [18] and Asiatic lions on a bold-shy axis between individuals raised in captivity and others that were wild-rescued [15]. Personality traits in African lions that correlate with subjective wellbeing indicate that their social structure is important for wellbeing, especially in terms of the Dominance structure found in this species. This suggests this dimension may be a prevalent trait among lions. [27]. For instance, lions 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 [35]. Lions with low scores for Dominance (affectionate, gentle, stable, submissive, and trusting) may be bullied and fail to thrive [17].

Agreeableness had the highest loadings for the behavioural traits aggressive to conspecifics, excitable, inquisitive, playful, smart and trusting, loading strongly and positively, while aggressive to people and irritable loaded negatively. The dimension of Agreeableness, though not discussed in the past for African lions, has been applied to other wild cats such as clouded leopards [14] and domestic cats [36]. 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 (excitable, inquisitive, playful, smart and trusting) are likely to represent cats that are coping well and potentially serve as a source of enrichment for other cats [36]. The Neuroticism dimension loaded positively for the traits of being anxious, clumsy, insecure, submissive and timid and loaded negatively for traits such as bold and dominant. These findings were similar to the findings of African lions who were rated on the sociability-neuroticism axis, indicating that members of the pride may be also be submissive, who may cope by hiding or avoiding interactions with other dominant animals [14, 32, 35].

Stress Physiology of lions at Zambi Wildlife Retreat and Sydney Zoo

In the literature, the levels of GCs may vary among individuals and these variations are influenced by the time of day, health status, age, sex, personality, body condition, time of year, stage of breeding and the environment (Vaz *et al.*, in press, [37]). Thus, even among lions managed in the same setting or among related individuals, there may be intraspecific metabolic variations in the GC levels [12, 38-40]. 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 [30, 41]. Thus, if the levels vary significantly and above the normal range of other individuals, it may reflect an imbalance [31]. Our results showed slight variations implying to animal individuality, but it did not vary significantly between individuals [42-44]. We assume that there was no significant variations in the GCs among the studied lions because they were all managed in similar settings without any additional stressors or ACTH challenge while conducting the study. For example, the eighteen lions at ZWR did not have visitors as compared to the four lions at SZ. Thus, our results support the literature that without additional challenges, the lions may not perceive stressors or be engaged in a coping style, and hence may not show significant variations in GC levels.

Factors influencing the personality dimensions and stress physiology of African lions

Our study assessed gender, age, core body temperature, origin and location of the 22 lions to determine any influence on their personality and stress physiology. On analysing the factors that could influence personality, we found the 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.* [14]. The lesser extent of Dominance among females could support their egalitarian behaviour in communal cub-raising because females are unable to influence the reproduction of other female pride members [45]. Previous studies have also suggested that males are more aggressive than females and the rates of social interaction correlate with group size [30]. Similarly, in other wild cats such as cheetahs, males scored significantly higher on the dominance and sociability dimensions than females [25].

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 [46], 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 [31] Sumatran tigers [33] and North American clouded leopards [12]. It is possible that our results could be influenced by the contraceptive implants in the studied females that could suppress the release of adrenocorticotropic hormone (ACTH) by the pituitary and decrease adrenal steroid output [47].

Secondly, our results revealed that the younger individuals, more specifically lions aged between 3-7 years, were significantly more dominant and agreeable than older lions aged between 8-15 years. These variations may reflect the role of sub-adults and adults within pride behaviours [18]. For example, among reintroduced African lions, the sub-adults are more likely to be alert than adults [18]. Similarly, tigers tend to be less aggressive and more friendly as they age [19]. However, other studies found no significance of age on personality dimensions of African lions [14] or cheetahs [25]. In snow leopards, variance in curious/playful and active/vigilant was highest among mid-aged animals and lowest in older animals. Variance in calm/self-assured was highest in the youngest animals and lowest in older animals, which adds to traits of agreeable individuals among different age groups [28]. We found no difference in Neuroticism between younger and older individuals. 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 [48].

Core body temperature, origin and location had no significant impact on the personality dimensions of the lions or on their GC levels. As felids spend most of their time resting and mostly in far proximity, it was difficult to measure the eye temperature accurately at all times. Hence, we took an average for the number of times we observed the lions [49, 50]. However, on hot days, the surface temperature of the lions would rise more than their core temperature, making it difficult to measure the eye from a distance. Thus, more precise validation and standardised techniques for assessing core body temperatures in lions are required. 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 S1) could have resulted in such an outcome.

Factors influencing the integrated relationship of personality and stress physiology

Building an understanding of the connections between personality and stress factors in African lions may help enhance their management and wellbeing. In this study, we found that on controlling age between personality types and stress levels, there was a strong partial negative relationship between Agreeableness and cortisol levels, with more agreeable lions having lower cortisol levels. This reveals that younger agreeable individuals may overcome challenges better than older, less agreeable lions. Younger lions may engage in more playful behaviours and show other carefree traits such as excitable, smart, trusting and aggression to conspecifics, which may also help them to get along with other members of the pride. They may also not be exposed to many challenges being younger, and hence may not perceive stressors as compared to older individuals [51]. Conversely, low scores for Agreeableness (aggressive to people and irritable) may reflect poor socialisation and frustration [30]; these traits may be related to underlying health conditions as found among rescued domestic cats [52] and having higher cortisol levels [53].

Previously, Ones *et al.* identified Agreeableness correlates weakly with Extraversion, is negatively related to Neuroticism and somewhat positively correlated to Conscientiousness [54]. In our study, the behavioural traits of neurotic lions, such as being anxious, insecure, submissive, and timid, seem to be the opposite of the agreeable lions. Neuroticism has been linked to poor coping abilities in humans and lions; lions with high scores for Neuroticism may be fearful of conspecifics or human presence, termed as social stress [32]. 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 [26, 55]. Although Neuroticism is most consistently related to negative stress outcomes in the literature, we did not find a significant relationship between neurotic individuals and cortisol levels in our study [14, 32]. This could be because the cortisol levels of the neurotic lions were measured under normal conditions, with no additional stressors or an ACTH challenge [56].

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. 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 by veterinarians to record health data.

As the commercial toolkits for stress hormone analysis are expensive, it would be ideal and useful to assess the stress cortisol levels at least once a year during veterinary procedures.

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 zoos. The advantages of this study can then be applied globally and help inform tailored animal welfare management, as well as exhibit design, conservation reintroduction programs, species survival recovery plans and in improving human-animal relationships.

Conclusions

In this study, three personality dimensions - Dominance, Agreeableness and Neuroticism were identified for African lions. We found gender and age strongly related to personality and stress physiology, emphasising the social organisation of lions where males and females of different age groups play an important role in shaping personality and stress. We also found lions that were rated higher for Agreeableness had lower cortisol levels under the influence of age. 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. Future research should focus on collating personality and stress data into the Zoological Information Management Software (ZIMS), so it is accessible to big cat caretakers around the world. This would assist in further understanding factors influencing personality and stress, and help improve individual and thus overall welfare for big cats.

Methods

Study sites and animals

Twenty-two African lions (13 males and 9 females) from two locations (Zambi Wildlife Retreat (ZWR) and Sydney Zoo (SZ)) were studied between June-August 2018 and May-December 2019 (Table S1). 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. Secondary demographic data about the lions was obtained from the study site records. Lion ages ranged between 3 and 16 years (*Mean* = 9.1, *SD* = 4.9), and the lions were housed with conspecifics, except one male whose sibling had passed away.

Personality assessment for captive African lions

Data collection

Wild cat personality questionnaires and focal animal observations were used to create the personality profiles of the lions [57, 58]. The questionnaire, comprising 52 behavioural traits, was used to rate the lion's personality (Table S2). 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. Each behavioural trait was defined for consistency in the raters' interpretation following previous felid personality assessments [14, 26, 32, 59]. 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. 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 [17, 60].

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 [61, 62]. Behavioural traits with confidence intervals overlapping zero were excluded from further analysis, as they were deemed unreliable. 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. Forty-four out of 52 behavioural traits passed Inter-rater Reliability testing across both study sites (Table S2). The reliabilities of mean ratings ICC (3, k) ranged from 0.30 (fearful of people) to 0.99 (erratic) for lions at ZWR and 0.60 (fearful of conspecific) to 0.99 (fearful of people & vocal) for lions at SZ.

Stress physiology assessment for captive African lions

Sample collection

Fresh faecal samples (< 2 days old) were identified from individual lions during behavioural observations and collected during husbandry or cleaning routines. Each sample was labelled and stored at −20 °C at the zoo and later placed in the −80 °C freezer for further analysis. These identified samples were opportunistically collected to determine average cortisol levels for each lion.

Hormone extraction and enzyme immunoassay (EIA)

Labelled frozen samples were placed in a freeze-drier (Alpha 1-4 LD plus) for 48 hours to obtain a dried sample [63]. 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 [64]. This supernatant solvent was then dried under nitrogen vapour (N_2) in a fumecupboard - 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.

A commercial cortisol EIA kit (96 well plate) from Arbor Assays was used to analyse the levels of faecal cortisol. The plate map was used to map the layout of the samples, controls, and standards. Following the supplier's instructions and previous studies on felids, 50 µL of standard and then 50 µL of samples were pipetted to the plate as per the plate map [13, 65]. Next, 75 µL of Assay Buffer was pipetted into the non-specific binding (NSB) wells. Further, 50 µL of Assay Buffer was pipetted into the maximum binding (B0 or Zero standard) wells. Using a multichannel pipette, 25 µL of cortisol conjugate was added to each well without disturbing it. Lastly, 25 µL of Cortisol Antibody was added to each well except the NSB wells. Sides of the plate were gently tapped, covered with a plate sealer and placed on a medium orbital shaker for an hour. The plate sealer was then removed, and the well plate was aspirated by washing each well with 300 µL of wash buffer 4 times in a plate washer and then dried by tapping the plate on clean paper towels.

A 100 µL of tetramethylbenzadine substrate was added to each well, which was further covered with a plate sealer and incubated at room temperature for 30 minutes. 50 µL of stop solution was then pipetted to each well, and the plate was placed in a plate 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.

Assay validation for lion faecal samples

All faecal samples were assayed in duplicates by taking two independent subsamples. 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% CIs = 0.67, 0.87). Further, parallel displacements were carried out between standard and sample hormones, to detect the relationship between predicted and test samples [66]. 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 [33]. The recovery of exogenous cortisol was added to the lion samples to analyse the efficiency of the faecal extracts ($R^2 = 0.9561$) (Fig. S1).

Investigating the factors influencing personality and stress physiology

Information on the gender, age, origin and location of the lions was obtained from zoo records (Table S1). To assess the core body 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 [67]. 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 [68]. The lions were observed every hour on observation days to ascertain each animal's average eye temperature.

Statistical Analysis

Extracting the Principal Components and determining personality dimensions

For the 44 behavioural traits that passed the ICC reliability test (Table S2), 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 [69]. We considered eigenvectors as being significant if the associated eigenvalues were greater than 1 [14, 36] and eigenvectors were extracted based on the correlation (not covariance) matrix. The unrotated PCA indicated that 9 factors accounted for 87.57% of the variation in lion behaviour (Table 1). 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 [14, 70-72] (Table S3). The parallel analysis reduced the 9 components to 3 components explaining 61.96% variation. Individual behaviours that had factors loading greater than (0.5) were viewed as biologically important behaviours that contribute to that eigenvector. The feline personality dimensions were then determined either by assessing the continuum of one personality dimension such as bold-shy [15] or by assessing multiple dimensions [14, 36]. These multiple dimensions modified from human personality studies on the Five-Factor Model (FFM) can be categorised as Openness to experience, Conscientiousness, Extraversion, Agreeableness and Neuroticism, abbreviated to OCEAN [73-75]. 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 [76, 77]. Thus, this current study used the multiple dimensions of the FFM and included Dominance for wild cats to ensure consistency in assessing big cat personality.

Determining the effects of gender, age, core body temperature, origin, and location on personality and stress physiology

We used a one-way analysis of variance (ANOVA) to examine the effects of gender, origin, and location on the PCA dimensions of African lions in SPSS. The level of significance, α, was set at 0.05. The PCA dimensions were set as the dependent factor and gender, origin, and location as independent. In addition, linear regression was used to determine the relationship between PCA dimensions and the age and core body temperature of the lions. The resulting PCA personality scores were further used in investigating the relationship between PCA dimensions and cortisol levels using a partial correlation. Figures were constructed using the "ggplot2" package in RStudio version 1.2.5033 (RStudio, Inc. Boston, MA).

Abbreviations

ACTH: Adrenocorticotropic hormone; CI: Class Intervals; EIA: Enzyme immunoassay; FFM: Five-Factor Model; GC: Glucocorticoid; ICC: Intra-class Correlation Coefficients; IRT: Infrared Thermal; NSB: Non-Specific Binding; OCEAN: Openness to Experience, Conscientiousness, Extraversion, Agreeableness, Neuroticism; PC: Principal Components; PCA: Principal Component Analysis; SZ: Sydney Zoo; ZIMS: Zoological Information Management Software; ZWR: Zambi Wildlife Retreat

Declarations

Ethics approval and consent to participate

The study was carried out using observational techniques. 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.

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.

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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.

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References

1.Richter SH, Hintze S. From the individual to the population – and back again? Emphasising the role of the individual in animal welfare science. Applied Animal Behaviour Science. 2019;212:1-8; doi:10.1016/j.applanim.2018.12.012.

2.Plan ALSS. Lion Care Manual. Association of Zoos and Aquariums. Silver Spring, MD2012. p. 143.

3.Wolfensohn S, Shotton J, Bowley H, Davies S, Thompson S, Justice WSM. Assessment of Welfare in Zoo Animals: Towards Optimum Quality of Life. Animals. 2018;8(7):110; doi:10.3390/ani8070110.

4.Gosling SD. From mice to men: What can we learn about personality from animal research? Psychological Bulletin. 2001;127(1):45-86.

5.Finkemeier M-A, Langbein J, Puppe B. Personality Research in Mammalian Farm Animals: Concepts, Measures, and Relationship to Welfare. Frontiers in Veterinary Science. 2018;5:131.

6.Koolhaas JM, Korte SM, De Boer SF, Van Der Vegt BJ, Van Reenen CG, Hopster H, et al. Coping styles in animals: current status in behavior and stress-physiology. Neuroscience & Biobehavioral Reviews. 1999;23(7):925-35; doi:10.1016/S0149-7634(99)00026-3.

7.Réale D, Dingemanse NJ. Animal Personality. eLS (encyclopedia of Life Science). Major Reference Works. Chichester: John Wiley and Sons Ltd; 2012.

8.Schneiderman N, Ironson G, Siegel SD. Stress and health: psychological, behavioral, and biological determinants. Annual review of clinical psychology. 2005;1:607-28; doi:10.1146/annurev.clinpsy.1.102803.144141.

9.Selye H. The evolution of the stress concept. American Scientist. 1973;61(6):692-9.

10.Narayan E, Baskaran N, Vaz J. Conservation Physiology of Tigers in Zoos: Integrating Stress Physiology and Behaviour to Monitor Their Health and Welfare. In: Singh KP, editor. Big Cats: IntechOpen; 2017.

11.Caramaschi D, Carere C, Sgoifo A, Koolhaas JM. Neuroendocrine and autonomic correlates of animal personalities. In: C. C, Maestripieri D, editors. Animal Personalities – Behavior, Physiology, and Evolution. Chicago, IL: The University of Chicago Press; 2013. p. 353–80.

12.Wielebnowski NC, Fletchall N, Carlstead K, Busso JM, Brown JL. Noninvasive assessment of adrenal activity associated with husbandry and behavioral factors in the North American clouded leopard population. Zoo Biology. 2002;21(1):77-98; doi:10.1002/zoo.10005.

13.Vaz J, Narayan EJ, Dileep Kumar R, Thenmozhi K, Thiyagesan K, Baskaran N. Prevalence and determinants of stereotypic behaviours and physiological stress among tigers and leopards in Indian zoos. PLoS ONE. 2017;12(4):e0174711; doi:10.1371/journal.pone.0174711.

14.Gartner MC, Powell DM, Weiss A. Personality structure in the domestic cat (Felis silvestris catus), Scottish wildcat (Felis silvestris grampia), clouded leopard (Neofelis nebulosa), snow leopard (Panthera uncia), and African lion (Panthera leo): a comparative study. Journal of Comparative Psychology. 2014;128(4):414-26; doi:10.1037/a0037104.

15.Goswami S, Tyagi PC, Malik PK, Pandit SJ, Kadivar RF, Fitzpatrick M, et al. Effects of personality and rearing-history on the welfare of captive Asiatic lions (Panthera leo persica). PeerJ. 2020;8; doi:10.7717/peerj.8425.

16.Kamyk CM. Boldness and natural behaviors in the African lion (Panthera leo): How are they related? Durham: University of New Hampshire; 2017.

17.Pastorino GQ, Viau A, Curone G, Pearce-Kelly P, Faustini M, Vigo D, et al. Role of Personality in Behavioral Responses to New Environments in Captive Asiatic Lions (Panthera leo persica). Veterinary Medicine International. 2017;2017:17; doi:10.1155/2017/6585380.

18.Dunston EJ, Abell J, Doyle RE, Evershed M, Freire R. Exploring African lion (Panthera leo) behavioural phenotypes: individual differences and correlations between sociality, boldness and behaviour. Journal of Ethology. 2016;34(3):277-90; doi:10.1007/s10164-016-0473-9.

19.Pastorino GQ, Paini F, Williams CL, Faustini M, Mazzola SM. Personality and Sociality in Captive Tigers (Panthera tigris). Annual Research & Review in Biology. 2017;21(2):1-17; doi:10.9734/ARRB/2017/38122.

20.Phillips C, Peck D. The effects of personality of keepers and tigers (Panthera tigris tigris) on their behaviour in an interactive zoo exhibit. Applied Animal Behaviour Science. 2007;106(4):244-58; doi:10.1016/j.applanim.2007.01.007.

21.Wang Q, Liu D, Holyoak M, Jia T, Yang S, Liu X, et al. Innate preference for native prey and personality implications in captive amur tigers. Applied Animal Behaviour Science. 2019;210:95-102; doi:10.1016/j.applanim.2018.10.006.

22.Boccacino D, Maia CM, Santos EF, Santori RT. Effects of environmental enrichments on the behaviors of four captive jaguars: Individuality matters. Oecologia Australis. 2018;22(1): 63–73; doi:10.4257/oeco.2018.2201.06.

23.Phillips C, Tribe A, Lisle A, Galloway TK, Hansen K. Keepers' rating of emotions in captive big cats, and their use in determining responses to different types of enrichment. Journal of Veterinary Behavior. 2017;20:22-30; doi:10.1016/j.jveb.2017.03.006.

24.Chadwick C. Social behaviour and personality assessment as a tool for improving the management of cheetahs (Acinonyx jubatus) in captivity. UK: University of Salford; 2014.

25.Baker Ka, Pullen PK. The Impact of housing and husbandry on the personality of cheetah (Acinonyx jubatus). Journal of Zoo and Aquarium Research. 2013;1(1):35-40.

26.Wielebnowski NC. Behavioral differences as predictors of breeding status in captive cheetahs. Zoo Biology. 1999;18(4):335-49; doi:10.1002/(SICI)1098-2361(1999)18:4<335::AID-ZOO8>3.0.CO;2-X.

27.Gartner MC, Powell DM, Weiss A. Comparison of Subjective Well-Being and Personality Assessments in the Clouded Leopard (Neofelis nebulosa), Snow Leopard (Panthera uncia), and African Lion (Panthera leo). Journal of Applied Animal Welfare Science. 2016;19(3):294-302; doi:10.1080/10888705.2016.1141057.

28.Gartner MC, Powell DM. Personality assessment in snow leopards (Uncia uncia). Zoo Biology. 2012;31(2):151-65; doi:10.1002/zoo.20385.

29.Sgambelluri E. Noninvasive Collection of Saliva in Panthera leo : Creation and Validation of a Novel Technique for Health Assessment in Captive African Lions (Panthera leo). New England: Antioch University; 2018.

30.Creel S, Christianson D, Schuette P. Glucocorticoid stress responses of lions in relationship to group composition, human land use, and proximity to people. Conservation Physiology. 2013;1(1):1-9; doi:10.1093/conphys/cot021.

31.Schildkraut R. Characteristation of positive welfare indices in captive African lions (Panthera leo). Australia: University of Sydney; 2016.

32.Torgerson-White L, Bennett C. Rating Methodology, Personality Axes, and Behavioral Plasticity: A Case Study in African Lions. Animal Behavior and Cognition. 2014;1(3):230-48; doi:10.12966/abc.08.02.2014.

33.Parnell T, Narayan EJ, Magrath MJL, Roe S, Clark G, Nicolson V, et al. Evaluating physiological stress in Sumatran tigers (Panthera tigris ssp. sumatrae) managed in Australian zoos. Conservation Physiology. 2014;2(1):cou038; doi:10.1093/conphys/cou038.

34.Gartner MC. Pet personality: A review. Personality and Individual Differences. 2015;75:102-13; doi:10.1016/j.paid.2014.10.042.

35.Heinsohn R, Packer C. Complex cooperative strategies in group-territorial African lions. Science. 1995;269(5228):1260; doi:10.1126/science.7652573.

36.Litchfield CA, Quinton G, Tindle H, Chiera B, Kikillus KH, Roetman P. The ‘Feline Five’: An exploration of personality in pet cats (Felis catus). PLOS ONE. 2017;12(8):e0183455; doi:10.1371/journal.pone.0183455.

37.Moberg G. Biological Response to Stress: Key to Assessment of Animal Well-Being? In: Moberg G, editor. Animal Stress1985. p. 27-49.

38.Zayan R. The specificity of social stress. Behavioural Processes. 1991;25(2):81-93; doi:10.1016/0376-6357(91)90011-N.

39.Carlstead K, Shepherdson D. Alleviating stress in zoo animals with environmental enrichment. In: Moberg GP, Mench JA, editors. The biology of animal stress: basic principles and implications for animal welfare2000.

40.Wasser SK, Hunt KE, Brown JL, Cooper K, Crockett CM, Bechert U, et al. A Generalized Fecal Glucocorticoid Assay for Use in a Diverse Array of Nondomestic Mammalian and Avian Species. General and Comparative Endocrinology. 2000;120(3):260-75; doi:10.1006/gcen.2000.7557.

41.Serres-Corral P, Fernández-Bellon H, Padilla-Solé P, Carbajal A, López-Béjar M. Evaluation of Fecal Glucocorticoid Metabolite Levels in Response to a Change in Social and Handling Conditions in African Lions (Panthera leo bleyenberghi). Animals. 2021;11(7); doi:10.3390/ani11071877.

42.Brown JL, Wasser SK, Wildt DE, Graham LH. Comparative Aspects of Steroid Hormone Metabolism and Ovarian Activity in Felids, Measured Noninvasively in Feces1. Biology of Reproduction. 1994;51(4):776-86; doi:10.1095/biolreprod51.4.776.

43.Schatz S, Palme R. Measurement of Faecal Cortisol Metabolites in Cats and Dogs: A Non-invasive Method for Evaluating Adrenocortical Function. Veterinary Research Communications. 2001;25(4):271-87; doi:10.1023/A:1010626608498.

44.Graham LH, Brown JL. Cortisol metabolism in the domestic cat and implications for non-invasive monitoring of adrenocortical function in endangered felids. Zoo Biology. 1996;15(1):71-82; doi:10.1002/(SICI)1098-2361(1996)15:1<71::AID-ZOO7>3.0.CO;2-9.

45.Packer C, Pusey AE, Eberly LE. Egalitarianism in Female African Lions. Science. 2001;293(5530):690-3.

46.Touma C, Palme R. Measuring Fecal Glucocorticoid Metabolites in Mammals and Birds: The Importance of Validation. Annals of the New York Academy of Sciences. 2005;1046(1):54-74; doi:10.1196/annals.1343.006.

47.Seal US, Barton R, Mather L, Olberding K, Plotka ED, Gray CW. Hormonal Contraception in Captive Female Lions (Panthera leo). The Journal of Zoo Animal Medicine. 1976;7(4):12-20; doi:10.2307/20094382.

48.Putman SB, Brown JL, Saffoe C, Franklin AD, Pukazhenthi BS. Linkage between fecal androgen and glucocorticoid metabolites, spermaturia, body weight and onset of puberty in male African lions (Panthera leo). PLOS ONE. 2019;14(7):e0217986; doi:10.1371/journal.pone.0217986.

49.Stryker J. Thermoregulatory Behaviour Assessment and Thermal Imaging of Large Felids. Ontario, Canada: The University of Guelph; 2016.

50.Gjendal K, Franco NH, Ottesen JL, Sørensen DB, Olsson IAS. Eye, body or tail? Thermography as a measure of stress in mice. Physiology & Behavior. 2018;196:135-43; doi:10.1016/j.physbeh.2018.08.022.

51.Antonevich AL, Rödel HG, Hudson R, Alekseeva GS, Erofeeva MN, Naidenko SV. Predictors of individual differences in play behavior in Eurasian lynx cubs. Journal of Zoology. 2020;311(1):56-65; doi:10.1111/jzo.12761.

52.Deary IJ, Weiss A, Batty GD. Intelligence and personality as predictors of illness and death: How researchers in differential psychology and chronic disease epidemiology are collaborating to understand and address health inequalities. Psychological Science in the Public Interest. 2010;11(2):53-79; doi:10.1177/1529100610387081.

53.Burgener N, Gusset M, Schmid H. Frustrated Appetitive Foraging Behavior, Stereotypic Pacing, and Fecal Glucocorticoid Levels in Snow Leopards (Uncia uncia) in the Zurich Zoo. Journal of Applied Animal Welfare Science. 2008;11(1):74-83; doi:10.1080/10888700701729254.

54.Ones DS, Viswesvaran C, Reiss AD. Role of social desirability in personality testing for personnel selection: The red herring. Journal of Applied Psychology. 1996;81(6):660-79; doi:10.1037/0021-9010.81.6.660.

55.Marinath L, Vaz J, Kumar D, Thiyagesan K, Baskaran N. Drivers of stereotypic behaviour and physiological stress among captive jungle cat (Felis chaus Schreber, 1777) in India. Physiology & Behavior. 2019;210:112651; doi:10.1016/j.physbeh.2019.112651.

56.Santymire RM, Freeman EW, Lonsdorf EV, Heintz MR, Armstrong DM. Using ACTH Challenges to Validate Techniques for Adrenocortical Activity Analysis in Various African Wildlife Species. International Journal of Animal and Veterinary Advances. 2012;4(2):99-108.

57.Gartner MC. Personality and Well---Being in Felids: Assessment and Applications to Captive Management and Conservation: The University of Edinburgh; 2013.

58.Highfill L, Hanbury D, Kristiansen R, Kuczaj S, Watson S. Rating vs. coding in animal personality research. Zoo Biology. 2010;29(4):509-16; doi:10.1002/zoo.20279.

59.Feaver J, Mendl M, Bateson P. A method for rating the individual distinctiveness of domestic cats. Animal Behaviour. 1986;34(4):1016-25; doi:10.1016/S0003-3472(86)80160-9.

60.Altmann J. Observational Study of Behavior: Sampling Methods. Behaviour. 1974;49(3/4):227-67.

61.Shrout PE, Fleiss JL. Intraclass correlations: Uses in assessing rater reliability. Psychological Bulletin. 1979;86(2):420-8; doi:10.1037/0033-2909.86.2.420.

62.Koo TK, Li MY. A Guideline of Selecting and Reporting Intraclass Correlation Coefficients for Reliability Research. J Chiropr Med. 2016;15(2):155-63; doi:10.1016/j.jcm.2016.02.012.

63.Hunt Kathleen E, Wasser Samuel K. Effect of Long-Term Preservation Methods on Fecal Glucocorticoid Concentrations of Grizzly Bear and African Elephant. Physiological and Biochemical Zoology. 2003;76(6):918-28; doi:10.1086/380209.

64.Palme R, Touma C, Arias N, Dominchin MF, Lepschy M. Steroid extraction: Get the best out of faecal samples. Vienna Veterinary Monthly Journal. 2013:238-46.

65.Narayan E, Parnell T, Clark G, Martin-Vegue P, Mucci A, Hero J. Faecal cortisol metabolites in Bengal (Panthera tigris tigris) and Sumatran tigers (Panthera tigris sumatrae). General and Comparative Endocrinology. 2013;194:318-25; doi:10.1016/j.ygcen.2013.10.002.

66.Baxter-Gilbert JH, Riley JL, Mastromonaco GF, Litzgus JD, Lesbarrères D. A novel technique to measure chronic levels of corticosterone in turtles living around a major roadway. Conservation Physiology. 2014;2(1):cou036; doi:10.1093/conphys/cou036.
67.Foster S, Ijichi C. The association between infrared thermal imagery of core eye temperature, personality, age and housing in cats. Applied Animal Behaviour Science. 2017;189:79-84; doi:10.1016/j.applanim.2017.01.004.
68.Jerem P, Jenni-Eiermann S, Herborn K, McKeegan D, McCafferty DJ, Nager RG. Eye region surface temperature reflects both energy reserves and circulating glucocorticoids in a wild bird. Scientific Reports. 2018;8(1):1907; doi:10.1038/s41598-018-20240-4.
69.Johnson RA, Wichern DW. Applied Multivariate Statistical Analysis 6th ed. USA: Pearson Education, Inc.; 2007.
70.Horn JL. A rationale and test for the number of factors in factor analysis. Psychometrika. 1965;30(2):179-85; doi:10.1007/BF02289447.
71.O'connor BP. SPSS and SAS programs for determining the number of components using parallel analysis and Velicer's MAP test. Behavior Research Methods, Instruments, & Computers. 2000;32(3):396-402; doi:10.3758/BF03200807.
72.Wood AM, Maltby J, Stewart N, Joseph S. Conceptualizing gratitude and appreciation as a unitary personality trait. Personality and Individual Differences. 2008;44(3):621-32; doi:https://doi.org/10.1016/j.paid.2007.09.028.
73.Digman JM. Personality structure: emergence of the five-factor model. Annu Rev Psychol. 1990;41:417-40.
74.Goldberg LR. The development of markers for the Big-Five factor structure. Psychological Assessment. 1992;4(1):26-42; doi:10.1037/1040-3590.4.1.26.
75.Goldberg LR. An alternative "description of personality": The Big-Five factor structure. Journal of Personality and Social Psychology. 1990;59(6):1216–29; doi:doi.org/10.1037/0022-3514.59.6.1216.
76.Gartner MC, Weiss A. Personality in felids: A review. Applied Animal Behaviour Science. 2013;144(1):1-13; doi:10.1016/j.applanim.2012.11.010.
77.King JE, Figueredo AJ. The Five-Factor Model plus Dominance in Chimpanzee Personality. Journal of Research in Personality. 1997;31(2):257-71; doi:10.1006/jrpe.1997.2179.

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

While the original PCA revealed 9 PCs with eigenvalues greater than 1, parallel analysis reduced this to the first three PCs.

	PC1 Dominance	**PC2 Agreeableness**	**PC3 Neuroticism**
Eigenvalue	13.765	9.176	4.322
% Variance	31.283	20.854	9.822
Loadings			
Active	**0.500**	**0.658**	0.022
Affectionate	-0.463	**0.694**	0.147
Aggressive to conspecifics	-0.064	**0.935**	0.130

Aggressive to people	**0.805**	-0.479	-0.174
Aimless	-0.007	0.353	0.030
Anxious	0.207	-0.132	**0.649**
Bold	**0.607**	0.182	**-0.537**
Bullying	**0.820**	-0.178	0.004
Calm	-0.244	0.271	-0.257
Clumsy	0.370	0.288	**0.541**
Cool	-0.394	**0.638**	-0.218
Cooperative	0.090	0.090	-0.279
Decisive	**0.649**	0.289	-0.284
Defiant	**0.707**	0.059	-0.148
Deliberate	**0.743**	**0.527**	-0.013
Distractible	0.473	**0.665**	0.370
Dominant	**0.633**	-0.011	**-0.571**
Eccentric	**0.605**	0.283	0.354
Erratic	**0.858**	-0.235	0.018
Excitable	0.328	**0.821**	0.13
Friendly to conspecifics	-0.442	**0.621**	0.134
Friendly to people	-0.397	**0.765**	0.120
Gentle	**-0.786**	0.453	0.015
Impulsive	**0.858**	0.272	0.159
Independent	0.416	-0.049	-0.288
Individualistic	**0.720**	0.396	0.043
Inquisitive	0.231	**0.715**	-0.248
Insecure	0.284	-0.201	**0.682**
Inventive	**0.649**	0.416	-0.047
Irritable	**0.789**	-0.413	-0.011
Jealous	**0.654**	0.286	0.318
Playful	0.399	**0.817**	0.036
Predictable	-0.348	0.194	0.112
Reckless	**0.936**	-0.082	0.099
Smart	**0.505**	**0.650**	-0.083
Solitary	**0.533**	-0.050	**0.507**
Stable	**-0.594**	**0.575**	-0.042
Stingy	**0.578**	-0.134	-0.363
Submissive	**-0.591**	-0.008	**0.620**
Tense	**0.697**	-0.081	0.493
Timid	-0.069	-0.167	**0.629**
Trusting	**-0.654**	**0.665**	-0.088
Vigilant	0.352	**0.612**	-0.313
Vocal	0.347	-0.198	0.164

Figures

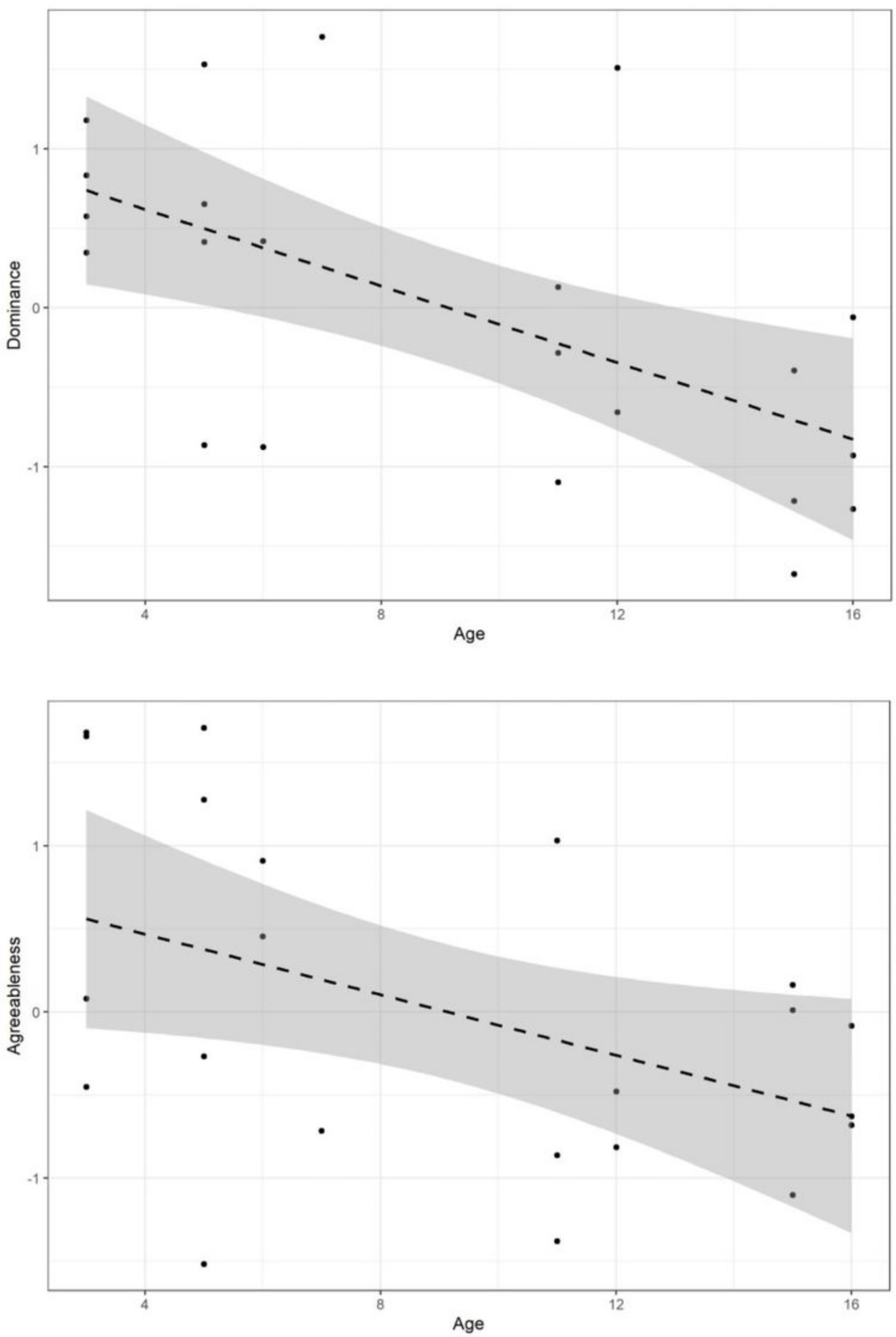

Figure 1

The negative relationship between lion age with Dominance (A) and Agreeableness (B) personality types

Supplementary Files