Effects of personality and life-history on the welfare of captive Asiatic lions (*Panthera leo persica*)

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Background

The long-term success of ex-situ conservation programmes depends on husbandry and enrichment practices complemented by a robust welfare assessment protocol. Most zoos and conservation programmes continue to employ a bottom-up approach to measure animal welfare that often fails to account for intraspecific variations. Despite accepting animal sentience, we are yet to address individuality and its role in governing animal welfare in captive conditions. We explored the role of individuality (personality traits, and life history) on behaviour-based welfare indices of 35 (14:21) captive Asiatic lions in Sakkarbaug Zoological Garden, Junagadh, India. We categorized the subjects based on personality traits (bold or shy), life history (wild-rescued or captive-raised) and gender, and compared welfare indices in the form of behavioural diversity, latency to novel objects, enclosure usage patterns and aberrant repetitive behaviours between the groups. Further, we assessed the inter-relationships between different behavioural measures of welfare.

Results

Our results show that intraspecific variations based on life history and personality traits consistently predict the welfare states of captive lions. Asiatic lions with bold traits (M=0.5, SD=0.12, n=21) and captive-raised life history (M=0.47, SD=0.12, n=16) used enclosure space more homogenously compared to shy (M=0.71, SD=0.15, n=14) and wild-rescued (M=0.67, SD=0.15, n=19) animals. Behaviour diversity was significantly higher in captive-raised (M=1.26, SD=0.3, n=16) and bold (M=1.23, SD=0.26, n=21) subjects compared to wild-rescued (M=0.83, SD=0.35, n=19) and shy (M=0.73, SD=0.34, n=14) individuals. On the other hand, aberrant repetitive behaviours (stereotypy) were significantly lower in bold (M=7.01, SD=3.9, n=21) and captive-raised (M = 7.74, SD = 5.3) individuals compared to wild-rescued (M=13.12, SD=6.25, n=19) and shy (M=16.13, SD=5.4, n=16) lions. Behaviour diversity was reliably predicted by the enclosure usage patterns and aberrant repetitive behaviours displayed by subjects. The enclosure usage pattern of subjects was predicted by their latency to novel objects, behaviour diversity, and age.

Discussion

Our findings underline the importance of individual-centric, behaviour-based, and multi-dimensional welfare assessment tools in ex-situ conservation programmes. The results suggest that behavioural welfare indices complemented with personality can help improve welfare of Asiatic lions and highlight the

critical need to address intraspecific variation in behavioural welfare measures in captive animals.

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Introduction

Welfare is defined as the balance between pathophysiology and affective states (Spruijt, Bos & Pijlman, 2001; Meehan & Mench, 2007; Boissy et al., 2007; Butterworth, Mench & Wielebnowski, 2011; Panksepp, 2011), or the state of the animal as it copes with its environment (Broom, 1991). Accurate welfare assessments are essential for long-term biopsychosocial health of captive animals housed in ex-situ conservation institutions (Engel, 1980; Korte, Olivier & Koolhaas, 2007; Broom, 2011). Animals housed under poor welfare conditions often suffer from allostatic overload, lose essential behaviour diversity, cognitive skills, and suffer from chronic stress (Sheperdson, Carlstead & Wielebnowski, 2004; Kroshko et al., 2016; Razal, Pisacane & Miller, 2016), affecting their overall survival and reproductive potential (Broom, 1991; Schreck, 2010). However, welfare assessments of captive animals pose unique challenges (Butterworth, Mench & Wielebnowski, 2011) as it encompasses both physical and psychological well-being (Brambell, 1965; Meehan & Mench, 2007; Panksepp, 2011). Significant body of research suggests personality traits (Izzo, Bashaw & Campbell, 2011; Watters & Powell, 2012), and early-life experiences (Butterworth, Mench & Wielebnowski, 2011) may predispose individuals to be more sensitive to changes in husbandry practices (Boissy & Erhard, 2014). Despite an urgent requirement of individual-centric welfare assessments for endangered species, most ex-situ facilities continue to employ a uni-dimensional approach where either of physiological, behavioural and keeper evaluations are used in such assessments (Watanabe, 2007; Butterworth, Mench & Wielebnowski, 2011). Ideally conservation breeding programs involving endangered species should account for individuality and address intraspecific variations during welfare assessments (Bracke & Hopster, 2006; Volpato et al., 2009; Rees, 2016) in zoological institutions.

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Asiatic lion (*Panthera leo persica*) is one such example of an endangered species that is relegated to a fraction of their historic range and currently found in the greater Gir landscape of Gujarat, India (Banerjee et al., 2013). With a global wild and captive population of about 523 and 359 individuals, respectively, (Srivastav, 2014; Pant, 2015) the future survival of Asiatic lions may depend on a successful conservation breeding program complemented by repatriation across historic ranges (Jhala et al., 2006; Meena, 2009). While extensive research on population ecology (Joslin, 1973; Jhala et al., 2009), behaviour (Meena, 2008), social dynamics (Meena, 2009; Chakrabarti & Jhala, 2017), and human-animal interaction (Joslin, 1973; Banerjee, Jhala & Pathak, 2010; Banerjee et al., 2013) of wild Asiatic lions has been conducted, the captive populations and their welfare needs have received relatively less attention. Pastorino et al., (2016, 2017) studied feline-keeper interactions, personality variations, and behavioural aspects of welfare in captive Asiatic lions at London zoo, but were limited by a small sample size (n=4) and a short study period. There is a paucity of information on detailed welfare status of captive Asiatic lions despite their presence across major global zoological institutions, and it is critical to evaluate and adopt the best welfare standards to meet long-term conservation goals for this species.

We studied 35 Asiatic lions housed in the ex-situ conservation breeding centre of Sakkarbaug Zoological Garden, Gujarat, India to understand how life history and personality influence behaviour-based welfare evaluations. Sakkarbaug zoo is the coordinating institution for the conservation breeding of Asiatic lion and hosted 47-60 individuals during 2015-2017. We categorized these subjects based on their life histories (wild-rescued vs. captive-raised), sex, and personality traits (bold vs. shy), and used species-typical behaviour diversity (Powell, 1995; Wemelsfelder et al., 2000; Rabin, 2003; Clark & Melfi, 2012; Miller, Pisacane & Vicino, 2016), space usage patterns (Kessel & Brent, 1996; Mallapur, Qureshi & Chellam, 2002; Ross & Shender, 2016), latency to novel objects (Murphy, 1977; Meehan & Mench, 2002; Sneddon, Braithwaite & Gentle, 2003), and proportion of aberrant behaviours (Mason, 2006; Tan et al., 2013; Japyassú & Malange, 2014; Kroshko et al., 2016) to assess the impacts of individual variations on welfare measures. We believe that such holistic welfare measurement will provide zoo managers an individual-focused welfare assessment tool to plan better husbandry practices in ex-situ conservation programs.

Materials & methods

Research permit and ethical considerations

Research permit for this study was granted by the Gujarat Forest Department, India (Permit no: WLP/28/A/1316-21/2015-16). This study complies with the regulations of zoo animal welfare standards set by the Central Zoo Authority, Government of India.

Study area

We conducted the study at Sakkarbaug Zoological Garden (SZG henceforth), which is situated within the natural range of Asiatic lions (*Panthera leo persica*). SZG is the coordinating zoo for the Asiatic lion conservation-breeding programme in India and hosts the largest captive population (n= 60) in the world (n=359). The zoo has a separate off-display conservation breeding facility, which houses 47 genetically diverse individuals sourced across the greater Gir landscape, Gujarat, India. This facility provided us a unique opportunity to study behaviour of wild-rescued and captive born lions under similar housing conditions. These animals are housed in large naturalistic enclosures that resemble the wild habitat of Asiatic lions. A map of the off-display conservation breeding enclosures of SZG is provided in Supplementary Figure 1.

Subjects and housing

We collected systematic data from 35 (14:21) healthy Asiatic lions housed in the off-display area of SZG. The study animals were either born in captivity (n=16; 3:13) or rescued from wild (n=19; 11:8). The subjects were housed in 13 enclosures spread across 8-ha area with a minimum of 500m^2 of space/animal. All enclosures had outdoor (paddocks) and indoor (retiring/feeding cells) areas (3m x 3m x 2m dimensions) with access to drinking water. Lions were brought inside their respective retiring/feeding cells at 1700 hours regularly for feeding and released back into the paddock at 2200 hours. All subjects were group-housed during the entire study duration. Some related females were iso-sexually paired and few males were housed with two related females. The enclosure size and husbandry practices were similar for all subjects. The animals were designated to specific groups of keepers, who trained them to respond to their house names and vocal instructions. Their diet included in-house slaughtered, quality-inspected buffalo meat. The animals were fed inside separate feeding cells from 1700-1900 hours daily. The average meat consumption was 3.5 kg (SD = 0.5 kg) for females (n=21) and 4.9 kg (SD = 1.4 kg) for males (n=14), with a starve day on every Sunday. The details of the study subjects are provided in Supplementary Table 1.

Study design

This study was conducted from July 2015 to January 2017. We assessed the behavioural effects of husbandry and management practices on captive Asiatic lions with different personalities and life histories. We conducted novel-object latency tests on subjects (Frost et al., 2007), followed by keeper interviews on a likert-scale based personality questionnaire that measured traits such as extraversion, openness to novel experience and activity (Allport and Allport, 1921; Gosling and John, 1999; Sloan Wilson et al., 1994). Subjects were grouped into different categories based on life histories (wild-rescued or captive-raised), personalities (bold-shy continuum), and sex (male or female). Individuals born in the zoo and rescued as cubs and hand-raised by keepers were categorized as captive-raised (n=16). Subjects that were rescued from the wild as adults were categorised as wild-rescued (n=19). We coded for personality traits of interest once at the beginning of the study and repeated after six months to check for trait consistency (Martin and Réale, 2008; Galhardo et al., 2012). For behaviour data collection, we used pre-existing ethogram for felids (Powell, 1995; Stanton, Sullivan & Fazio, 2015) and modified it to include unique behaviours displayed by subjects (Supplementary Table 2). Two independent observers collected all behaviour data. To minimize inter-observer bias, behaviour recording was commenced after inter-observer reliability reached satisfactory levels from the same group of animals (Cronbach's $\alpha > 0.8$) (Gliem & Gliem, 2003). We recorded behaviour at three different time periods: 0500-1100 hours, 1300-1800 hours and 2200-0500 hours. We used a combination of instantaneous scan sampling and focal animal sampling to collect behavioural data (Altmann, 1974; Mason & Mendl, 2007). We recorded instantaneous scan at one-minute intervals for one-hour duration followed by a 15-minute rest to mitigate observer fatigue. During each scan, we recorded the behavioural state of the subject and its location in the enclosure. We measured the directionality of all social interactions between subjects. We conducted focal animal sampling through video recordings to accurately measure durations of social, and aberrant repetitive behaviours (Martin & Bateson, 1993). We collected data on the following parameters:

Personality assessment and latency to novel objects

Personality is defined as the consistent difference between individuals in their behaviour across time and contexts (Réale et al., 2007; Franks, Higgins & Champagne, 2014). Personality is related to an individual's coping style and often determines its response to welfare concerns in captivity (Koolhaas et al., 1999; Moneta & Spada, 2009; Melotti et al., 2011; Gartner, Powell & Weiss, 2016). Personality traits of individual animals determine their decision-making skills which contribute to survival success in the wild (Coelho, de Azevedo & Young, 2012; Carter et al., 2013; Franks et al., 2013; Owen, Swaisgood & Blumstein, 2017), and thus can be useful in welfare measures (Rouff, Sussman & Strube, 2005). Personality assessments based solely on keeper evaluations can be biased due to keeper-animal associations (Broom, 1991; Mills, 1998; Gartner, Powell & Weiss, 2016). To ensure consistency and reliability in personality assessment, we adopted a combination of rating and coding (Funder & Colvin, 1988; Funder, 1995; Gosling & Vazire, 2002; Highfill et al., 2010). We assessed subjects on bold-shy continuum of personality, as it is an important indicator of cognitive performance (Sloan Wilson et al., 1994; Highfill et al., 2010; Coelho, de Azevedo & Young, 2012; Chadwick, 2014). Experienced keepers rated subjects on a scale of 1-9 for pre-selected personality traits on the bold-shy continuum (Supplementary Table 3). To validate the keeper ratings, we conducted personality tests in day kraals for ten minutes using video recorders in the absence of keepers and observers. During these tests, the subject was (a) observed interacting with conspecifics in its enclosure; (b) approached by an unknown person; and (c) was exposed to non-food novel objects (lion-sam ball, and bungee cord). Naive observers with no prior exposure to study subjects coded the behaviour of subjects corresponding to personality traits under consideration i.e. boldness and shyness. Observers also recorded the time taken in seconds (latency value) for subjects to touch novel objects or approach unknown person (Sih, Bell & Johnson, 2004; Frost et al., 2007). The percentage of time spent by animals in bold (extroversion or curious) vs. shy (wary or afraid) behaviour was measured.

We repeated the novel object tests after a month to check for trait consistency, and an average of the latency values was calculated for each subject. Observers grouped subjects into bold and shy categories based on a comparison between the proportion of bold and shy behaviours performed by subjects across all trials. We found that keepers (n=3) and observers (n=3) reliably agreed on the personality type (Cronbach's alpha > 0.9) of subjects (bold-shy continuum).

Enclosure usage pattern

Enclosure usage pattern is a critical behavioural parameter that is influenced by the biological relevance of different zones of the captive environment (Traylor-Holzer & Fritz, 1985; Plowman, 2003; Rose & Robert, 2013; Ross & Shender, 2016). Although large naturalistic enclosures are necessary for good welfare, enclosure usage should be closely monitored to evaluate their functionality (Mallapur, Qureshi & Chellam, 2002; Rose & Robert, 2013). We divided each enclosure into ten equal zones, which included three broad zones viz. a) proximal, b) medial, and c) distal zones. Each of these broad zones was further subdivided into three smaller zones as i) left, ii) middle, and iii) right. The tenth zone was the paddock area next to the retiring cell (Figure 1). We recorded the enclosure zone location of subjects during each scan.

Species-typical behaviour diversity

We used a combination of instantaneous scan sampling and focal animal sampling (Altmann, 1974; Gilby, Pokempner & Wrangham, 2010) to record lion behaviour patterns in captivity. During each scan, we recorded detailed behavioural states (Supplementary Table 3) of the lion and the enclosure zone in which it was located. In case the subject was performing a social behaviour or aberrant repetitive behaviours (ARBs), we recorded the duration and directionality of the behaviour along with the name of participants. We used a double observer method to standardize behaviour sampling strategy and reduce inter-observer bias. To increase inter-observer reliability (Caro et al., 1979) both observers recorded the behaviour patterns of same subjects independently for three consecutive day until agreeability ratings increased to acceptable levels (Cronbach's $\alpha > 0.9$). We gathered a total of 2,009 hours of behaviour observation data (average data of 57 hours/ subject) across 486 observation days.

Aberrant repetitive behaviours (ARB)

Aberrant repetitive behaviours (ARB) are reliable indicators of poor welfare conditions (Dawkins & Hill, 2004; Watters, 2009; Kroshko et al., 2016). Repetitive behaviours are indicative of changes in neurophysiology and cognitive dysfunction (Muehlmann & Lewis, 2012). We calculated the proportion of ARBs displayed by each subject per session. ARBs mostly included, stereotypic swaying, pacing, and nose rubbing behaviours (Supplementary Table 3). We did not record displacement behaviours such as pacing performed before feeding, or while interacting with conspecifics housed in adjacent enclosures as ARB. We considered behaviours persisting over five consecutive scans and without a valid cause as ARB. We calculated the proportion of scans spent by each subject performing ARBs as an indicator of poor welfare (Mason & Latham, 2004).

Hypothesis

We tested three hypotheses on how behavioural welfare measures might vary among different groups of captive Asiatic lions housed under similar conditions. Our first hypothesis was that there would be no variations in behavioural welfare measures between male and female subjects and the measures would perform reliably for both sexes. Our second hypothesis was that the wild-rescued lions would display more diverse measures of behavioural welfare compared to captive-raised animals. Our final hypothesis was that individuals with shy personality would show less diversity in behavioural welfare measures compared to bold individuals.

Data analysis

We categorized the subjects (n= 35) into six groups based on their personality (bold=21, shy=14), life history experiences (captive-raised=16, wild-rescued=19) and sex classes (male=14 and female=21) and all six groups served as independent categorical variables. We measured different indices of welfare such as enclosure space usage (SPI), behaviour diversity (SWI), latency to novel objects, and aberrant repetitive behaviours as dependent variables for downstream analyses. We conducted all analyses with R version 3.4 and 3.5 through RStudio (RStudio, 2012) using packages, dplyr (Wickham & Francois, 2016), ggplot2 (RStudio, 2015), lm, lubridate (Spinu, Grolemund & Wickham, 2018), tidyverse (Wickham, 2017), and funModeling. For exploratory data analyses we used Shapiro-Wilk test and Levene's test to ascertain the normal distribution and homogeneity of variance in SPI, SWI, latency and ARB values, respectively, and conducted bivariate Pearson's correlation. We compared welfare indices between groups using independent samples t-test. When comparing between means of two groups with different sample sizes, it is important to report effect sizes in addition to p-values to indicate the scale independent degree of difference. We calculated effect sizes to quantify differences in welfare measures between groups (Cohen, 1992; Lakens, 2013).

Finally, we explored causative inter-relationships between latency to novel objects, aberrant repetitive behaviours (ARB), behaviour diversity (SWI) and enclosure usage patterns (SPI). We conducted three linear regression (univariate) using enclosure space usage, behaviour diversity, aberrant behaviours (ARB) as dependent and predictor variables interchangeably. Before conducting regression analysis, we checked for multicollinearity between predictor variables using measures of VIF (variance inflation factor). If two variables showed a high level of correlation, we avoided using them as predictors in a regression model.

Personality and latency to novel object

We used a combination of behavioural coding and personality-rating instrument (Highfill et al., 2010) to ascertain personality profile of subjects, which considered aggression levels, activity, boldness, curiosity and level of stereotypy (King & Figueredo, 1997). We asked three zookeepers to rate subjects on a likert scale of 1-9 for measures of personality traits based on bold and shy continuum.

We measured the latency of each subject to react to non-food novel objects over the course of two trials with different non-food novel objects (i.e. a ball and a rope). We categorized subjects as bold or shy based on the proportion of bold and shy behaviours performed during the tests. For all 35 subjects, the keeper ratings agreed with the conclusions drawn by observers based on novel-stimulus tests (Cronbach's $\alpha > 0.9$). Based on personality tests, and keeper rating, we categorized 21 subjects (10:11) as bold and 14 subjects (4:10) as shy. We found that latency measures were not normally distributed across subjects, therefore we used non-parametric statistics (Kolmogorov Smirnov test) to compare the means of latency values between subjects of different personality types, life history, and sex.

Enclosure usage pattern

We calculated the spread of participation index (SPI) (Plowman, 2003) of enclosure usage for all 35 subjects across 486 observation days using instantaneous scan data. We conducted independent-samples t-test between different groups of subjects followed by multiple regressions to understand the interconnection of different welfare indices. We calculated the SPI values using the following formula:

$$SPI=\frac{\Sigma|fo - fe|}{2(N - femin)}$$

where f_o stands for observed frequency of usage of enclosure zones, f_e stands for expected frequency of enclosure usage. N stands for total number of observations in all zones of the enclosure and f_{emin} stands for the expected frequency of observation for the smallest zone (Plowman, 2003). SPI measures indicate the homogeneity of space usage patterns. A high SPI value (close to 1) indicates that subjects are biased towards certain areas of the enclosure, while a lower SPI value (close to 0.5 or lower) indicates that lions use most areas of the enclosure equitably.

Species-typical behaviour diversity

We used Shannon-Weiner diversity index (SWI) to measure species-typical behaviour diversity as this approach considers both richness and evenness of species-typical behaviours in the data set (Clark & Melfi, 2012; Miller, Pisacane & Vicino, 2016; Spiezio et al., 2018). We compiled an ethogram of all behaviour states and events observed from all subjects during the study period (Supplementary Table 3). We pooled all behaviour observations of each subject to calculate behaviour diversity. We excluded aberrant repetitive behaviours from the calculations, since they did not qualify as species-typical behaviours. We employed t-test to compare the means between subjects belonging to different life histories, personality types, and sex.

Aberrant repetitive behaviours

We counted the total number scans of ARBs displayed by each subject during every study session. We calculated proportion of ARBs displayed across the entire study period by each subject and used that as a continuous variable to compare across different categories of subjects based on their age, sex, life history, and personality. We used t-tests, and multiple regression analysis to explore the relationship between various welfare indices.

Results

Latency to novel object

The mean latency for all subjects after averaging both observations (six months apart) was 47.76 seconds (SD=46.85). Captive-raised individuals showed significantly lower latency to novel objects (M=18.61, SD=21.55, n=16) compared to wild-rescued individuals (M=72.30, SD=48.7, n=19) with effect size (Cohen's d) of 1.49 (Table 1, Figure 2). Bold animals showed significantly lower latency to novel objects (M=11.13, SD=3.65, n=21) compared to shy individuals (M=102.71, SD=17.4, n=14), with a high effect size (Cohen's d = 7.508) (Table 1, Figure 2). Our gender-based comparative analyses revealed no difference in latency scores between male (M= 37.02, SD= 45, n=14) and female (M=54.9, SD=47.8, n=21) subjects (Cohen's d = 0.38) subjects.

We found that latency to novel objects was positively correlated (Supplementary Figure 2, Table 2) to enclosure usage (SPI values) index (r=0.6, n=35, p=0.00), and proportion of aberrant repetitive behaviours (r=0.53, n=35, p=0.00). Latency was negatively correlated to behaviour diversity (r=-0.58, n= 35, p=0.00). We did not conduct linear regression analysis to ascertain its relationship with other welfare indices, as the latency values were not normally distributed.

Enclosure usage

Enclosure space usage pattern varied significantly between subjects with different personality types and life history parameters. Wild-rescued individuals used enclosure space less homogeneously (M=0.67, SD=0.15, n=19) than captive-born individuals (M=0.47, SD=0.12, n=16) (t (33) =4.28, p=0.0001, Cohen's d=1.47) (Table 1, Figure 2). Bold subjects had significantly lower SPI scores signifying homogenous enclosure use (M=0.5, SD=0.12, n=21) compared to shy individuals (Table 1, Figure 2) (M=0.71, SD=0.15, n=14) (t (33) =-4.572, p=

0.0001, Cohen's d=1.54). Overall, the SPI value of males (M=0.61, SD=0.20, n=14) was not significantly different from female (M=0.57, SD=0.15, n=21) lions (t (33) = 5.28, p = 0.6).

Enclosure usage (SPI values) is positively correlated (Supplementary Figure 2, Table 2) with latency values (r=0.6, p=0.00), and proportion of ARBs (r= 0.53, p= 0.001). Enclosure usage is negatively correlated with behaviour diversity (r=-0.61, p=0.001). As aberrant repetitive behaviour and behaviour diversity were highly correlated, we avoided using them together as predictors for regression analyses. Multiple regression analyses revealed that behaviour diversity, latency to novel object, and age of subject explained 66% of the variance in enclosure space usage (R^2=0.66, F (3, 31) = 20.66, p <0.001) (Table 3). The predicted regression equation for enclosure usage is SPI = -0.64 +(-0.21) x (Behaviour diversity) +(3.7e-5) x (age in days) + (1.3e-03) x (Latency). From the regression analysis we can infer that younger subjects used enclosure evenly compared to older subjects. Higher latency to novel objects can also correspond to low enclosure space use. Furthermore, subjects that use the enclosure space evenly are likely to have a diverse species-typical behaviour repertoire.

Species-typical behaviour diversity

We found that species-typical behaviour diversity of captive-raised animals (M=1.26, SD=0.3, n=16) was higher than wild-rescued animals (M=0.83, SD=0.35, n=19) (t (33) =-3.94, p=0.001, Cohen's d=1.35) (Table 1, Figure 2). Further, bold animals had higher behaviour diversity (M=1.23, SD=0.26, n=21) than shy individuals (M=0.73, SD=0.34, n=14) (t (33) = 4.897, p=0.0001, Cohen's d=1.64) (Table 1, Figure 2). However, there was no significant difference in the diversity of species-typical behaviours between male (M=0.96, SD=0.43, n=14) and female (M=1.1, SD=0.35, n =21) lions (t (33) = -0.85, p = 0.4).

Behaviour diversity was negatively correlated with latency to novel objects, (r=-0.59, p=0.01), aberrant repetitive behaviours (r=0.884, p=0.01), and enclosure usage (r=-0.61, p=0.01) (Supplementary Figure 2, Table 2). Multiple regression analyses indicated that latency to novel objects, space usage patterns and age of subjects explained 53% of the variance in the behaviour diversity (R^2=0.85, F (2,32) = 90.92, p<0.001) (Table 3). The predicted regression equation is Behaviour diversity = 1.8 + (-0.046) x (Aberrant repetitive behaviour) + (-0.46) x (Enclosure usage). The results from the linear regression indicate that subjects that show less ARB and use enclosure space more homogenously are likely to have higher behaviour diversity.

Aberrant repetitive behaviours (ARB)

Proportion of aberrant repetitive behaviours (ARBs) varied between wild-rescued individuals (M=13.12, SD=6.25, n=19) than captive-raised individuals (M=7.74, SD=5.3, n=16) (t (33) =2.71, p=0.01, Cohen's d=0.92) (Table 1, Figure 2). Bold individuals (n=21) showed significantly lower amount of stereotypic behaviour such as pacing and swaying (M=7.01, SD=4, n=21) compared to shy individuals (M=16.13, SD=5.4, n=14) (t (33) =-5.82, p=0.000, Cohen's d=1.94) (Table 1, Figure 2). We found no variation in expression of stereotypic behaviour between male (M=11.04, SD=7.05, n=14) and female (M=10.41, SD=6.02, n=21) subjects (t (33) =0.282, p=0.78, Cohen's d = 0.09).

ARB was positively correlated with latency to novel objects (r=0.57, p=0.01), and enclosure usage (r = 0.54, p =0.01) but was negatively correlated with behaviour diversity (r=-0.88, p=0.01) (Supplementary Figure 2, Table 2). Regression analysis explained 85% of variance in ARB values with behaviour diversity and age as the significant predictor variables (R^2=0.85, F (2,32) = 90.27, p=0.000) (Table 3). The predicted regression equation for aberrant repetitive behaviour is, ARB = 28.08 + (-15.05) x (behaviour diversity) + (-6.7e-04) x (age in days). From the regression analysis we can assert that subjects displaying a higher diversity of species-typical behaviours were less likely to show ARBs. Interestingly, age had a miniscule yet statistically significant effect on ARBs, implying that younger individuals were more likely to show such behaviours.

Discussion

To the best of our knowledge, this is the first study to compare the behavioural welfare measures of wild-rescued and captive-raised Asiatic lions with differing personality traits in an empirical framework. Our sample size constitutes 10% of the global captive stock and 6% of the wild population of Asiatic lions, making the results relevant for the global conservation initiatives for this species. The results clearly show that personality and life history significantly affect behavioural welfare measures. We did not observe any sex-specific variations in behavioural welfare measures of the subjects, confirming our first hypothesis. However, contrary to our second hypothesis, wild-rescued lions showed low behaviour diversity, high enclosure-use bias, increased stereotypy, and higher latency to novel objects compared to captive-raised subjects. Since most wild-origin lions were rescued as adults, we believe that they were unable to perform diverse array of species-typical behaviours due to the lack of sufficient cognitive stimulus in captivity. We also found that most wild-rescued individuals have shy personality traits (n=12), whereas majority of captive-raised individuals have bold traits (n=14). Finally, our results supported the third hypothesis that captive-raised lions with bold personalities are more resilient to small changes in welfare conditions than shy subjects. We found that behaviour diversity of Asiatic lions had a strong linear relationship with proportion of aberrant repetitive behaviours along with enclosure usage patterns. Therefore, animals with low behaviour diversity were highly likely to display more ARBs and show more enclosure zone bias. Existing studies suggest that the inability to perform instinctive and habitual behaviours might result in allostatic overload (Korte, Olivier & Koolhaas, 2007). However, it is important to point out that the proportion of ARBs differed significantly between wild-rescued and captive-raised lions. This means that the inability to perform species-typical behaviours translates into an increase in stereotypy and timely intervention and improvement of husbandry practices would lead to better welfare to wild-rescued, and shy animals. Overall, Asiatic lions with different personality traits (bold and shy) and life-history (captive-raised and wild-rescued) significantly differed on measures of welfare, which supports earlier studies (Japyassú & Malange, 2014) on animal individuality.

These results may misconstrue that wild-rescued lions and those with shy personality traits are condemned to suffer more in captivity. On the contrary, our results simply indicate the need for different husbandry practices, enclosure design, and enrichment interventions for animals with differing life histories and personality traits. Zoo managers and biologists should address the welfare needs of individuals to meet conservation goals through tailored-husbandry practices and individual-centric welfare measures to create a richer cognitive experience for wild-rescued and shy animals.

Animal welfare as a discipline has its foundations in ethical concerns for animals but has slowly embraced the scientific concept from animal ecology, behaviour and physiology (Broom, 1991; Fraser, 1999). Modern welfare science uses animal behaviour in the subjective context of affective states of animals to create opportunities for positive emotions (Dawkins, 2004; Fraser, 2009; Whitham & Miller, 2016). The impacts of welfare are far-reaching as it affects cognitive performance (Harding, Paul & Mendl, 2004; Broom, 2011; Boissy & Erhard, 2014), behaviour diversity (Rabin, 2003; Greggor et al., 2016) and affective states (Mendl et al., 2009; Whitham & Miller, 2016) of animals. Good welfare practices are vital for the success of an ex-situ conservation programme (Rabin, 2003; Teixeira et al., 2007; Broom, 2011). Existing research on animal personality posits that bold and shyness are important attributes that can provide survival value to animals (Bremner-Harrison, Prodohl & Elwood, 2004). Early life experiences can alter the personality state of animals (Higley et al., 1991; Frost et al., 2007; Watters & Powell, 2012) which can lead to intraspecific variation in welfare requirements. Recent studies also indicate a strong inter-relationship between personality and cognition with implications in ex-situ conservation programme success (Watters & Powell, 2012; Gartner, Powell & Weiss, 2016) as personality traits determine the umwelt of individuals and affect cognition, affective states, and ultimately welfare (Carere & Locurto, 2011; Izzo, Bashaw & Campbell, 2011; Boissy & Erhard, 2014). Our findings support this theory in Asiatic lions, where animals with different personality traits significantly differ on behavioural measures of welfare under similar housing conditions.

In this study, we also explored the inter-relationship between different welfare indices. We found that subjects that used enclosure space homogenously and displayed less ARBs were more likely to show diverse behaviour repertoire, which was supported by existing studies (Wemelsfelder et al., 2000; Clark & Melfi, 2012). We found that latency to novel objects is positively correlated to stereotypy and enclosure usage bias (Wemelsfelder et al., 2000; Sneddon, Braithwaite & Gentle, 2003; Watters, Margulis & Atsalis, 2009) and negatively correlated to behaviour diversity. Latency measure is an important tool for managers to evaluate the welfare condition of animals. Our regression models show that evenness of enclosure usage was determined by the age of subjects, latency to novel objects, and behaviour diversity of subjects. Proportion of ARBs and behaviour diversity was highly negatively correlated, which presents a strong case for zoo managers to increase the gamut of sensory stimuli available for captive animals to display natural behaviours (Swaisgood & Shepherdson, 2005). All four behavioural welfare measures used in this study was significantly affected by personality and life-history parameters of the subjects. Moreover, bivariate correlation and regression models underlined strong inter-linkages between all welfare indices (Rabin, 2003; Rose & Robert, 2013; Kroshko et al., 2016). To reiterate, Asiatic lions have diverse intraspecific variations that lead to statistically significant behavioural welfare measures under similar husbandry protocols.

Felids are among the most represented taxa across zoological institutions, which necessitates a uniform welfare index to evaluate captive conditions (Szokalski, Litchfield & Foster, 2013). Welfare assessments validated through this study such as personality assessments, latency, enclosure usage, and behavioural diversity can be useful, cost-effective, and non-invasive tools to diagnose and prevent zoochosis in captive wild animals (Broom, 1991; Mason & Mendl, 2007). Ex-situ conservation breeding programmes aim to create a line of genetically healthy and behaviourally diverse stock of animals that can successfully recolonize wild habitats (Keulartz, 2015). Studies show that regular individual-centric welfare assessments are necessary for long-term goals of ex-situ conservation breeding programmes (Whitehouse et al., 2013; Cannon et al., 2016; Whitham & Miller, 2016). Our results underline an urgent need for managers to implement welfare assessment protocols that measure animal cognition, behaviour diversity, and functionality of captive environment, which can lead to individual-specific husbandry practices. To achieve this objective, we must optimize captive environment and management practices to ensure good animal welfare in ex-situ conservation programmes (Reading, Miller & Shepherdson, 2013; Moorhouse et al., 2015). We hope that this study encourages managers and biologists to revisit traditional husbandry protocols and optimize them to the cognitive needs of individual animals under their care.

Conclusion

Optimized animal welfare practices are a prerequisite of every ex-situ conservation programme. A significant corpus of animal welfare research focuses on the prevention and amelioration of negative emotions in captive individuals. The first major stepping stone in animal welfare research was acceptance of animals as sentient beings capable of suffering (Dawkins, 1990; McMahon et al., 2013). The current philosophy of animal welfare has been galvanized in ethology (Hediger, 1968), positivism (Mendl et al., 2009; Fraser, 2009), and affective states (Dawkins, 1990; Fraser & Duncan, 1998; Bateson & Matheson, 2007; Fraser, 2009). Acknowledging individual personalities and welfare requirements must be the next logical step to increase behaviour diversity in ex-situ conservation breeding programmes (Martin-Wintle et al., 2017). Modem ex-situ conservation facilities must create opportunities for individuals to experience positive emotions, which ultimately lead to better biopsychosocial health. As shown in our study, similar husbandry practices may lead to various welfare outcomes due to intraspecific differences. Ex-situ conservation should focus on welfare requirement of individual animals, in consonance with long-term goals. We encourage zoo management to address welfare deficits by employing personality, life history, and behavioural indices. This study emphasizes the dire requirement for individual-centric welfare measurement indices for all animals at ex-situ conservation breeding centers and on-display enclosures. Long-term sustenance of endangered species must be achieved by the combination of optimized ex-situ and in-situ conservation measures also known as the “one-plan approach” (Schwitzer et al., 2013). Based on the results from this study, we propose to facilitate tailored husbandry and enrichment practices at ex-situ institutions to conserve cognitive capabilities of captive animals. We believe that this study elucidates the importance of personality-based approach to welfare assessment in ex-situ conservation institutions and paves way for a wider utilization of these techniques by managers and biologists.

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Figure legends

Figure 1: Schematic representation of an enclosure in Sakkarbaug zoological garden with the layout of zones for behavioural observations of enclosure use by study subjects.

Figure 2: Comparison of behavioural welfare indices of Asiatic lions across personality (bold and shy), life-history (wild and captive) and gender (male and female) categories. The behavioural welfare indices used here are a) Enclosure usage; b) Behaviour diversity; c) Aberrant repetitive behaviour; and d) Latency to novel objects.

Figure 1

Schematic representation of an enclosure in Sakkarbaug zoological garden with the layout of zones for behavioural observations of enclosure use by study subjects.

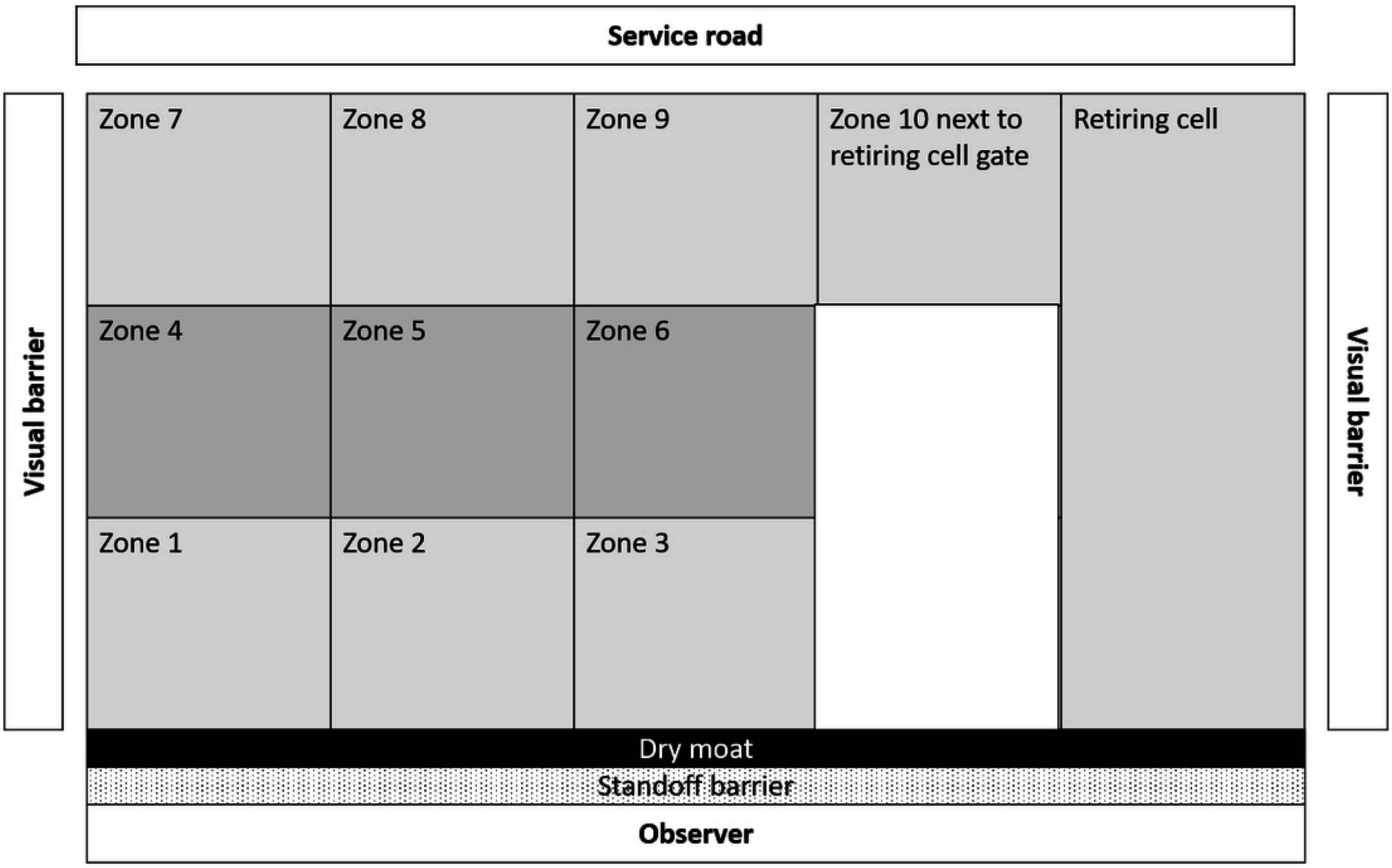

Figure 2

Comparison of behavioural welfare indices of Asiatic lions across personality (bold and shy), life-history (wild and captive) and gender (male and female) categories.

The behavioural welfare indices used here are a) Enclosure usage; b) Behaviour diversity; c) Aberrant repetitive behaviour; and d) Latency to novel objects.

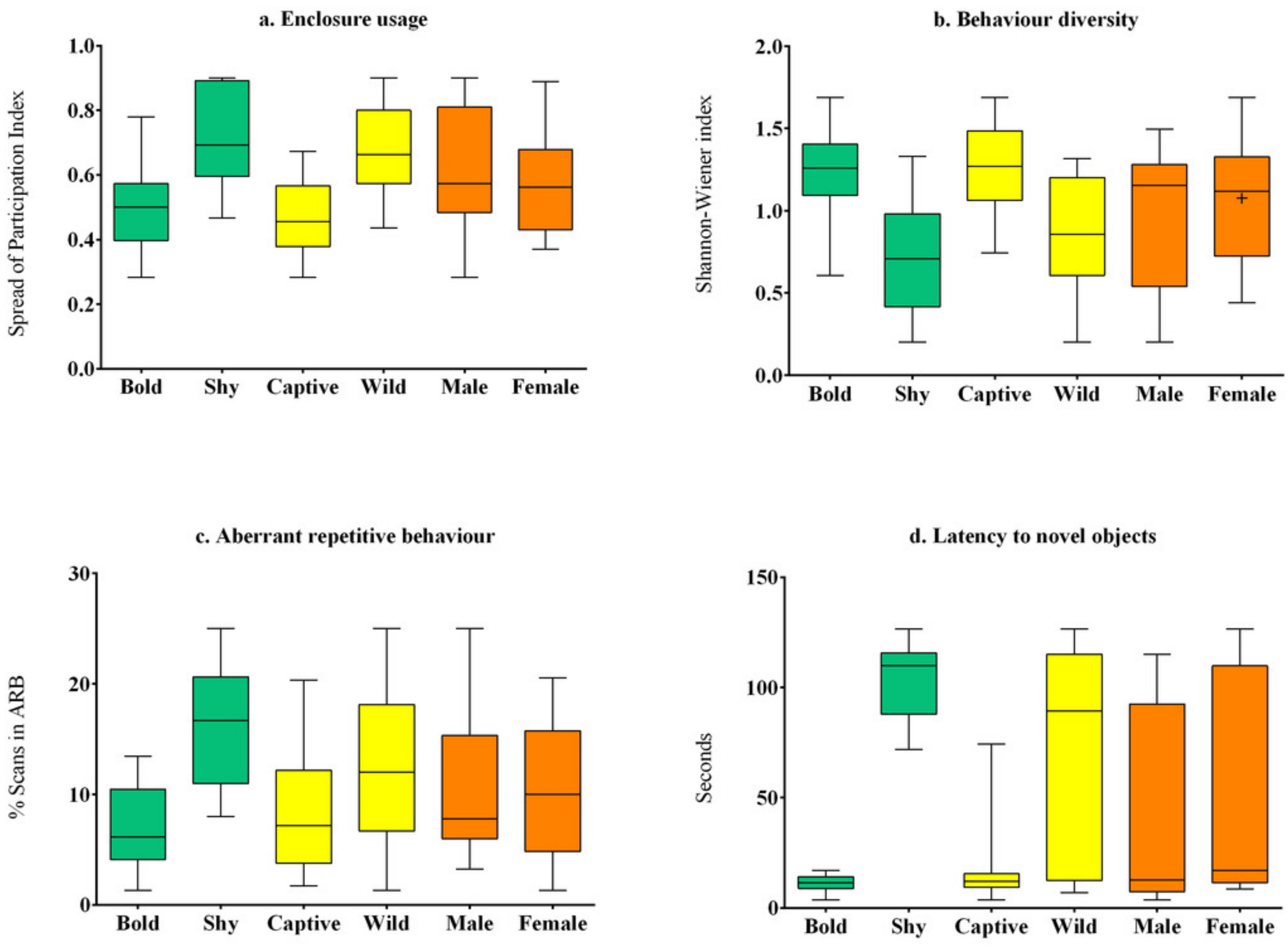

Table 1(on next page)

Comparison of welfare indices between captive-born and wild-rescued Asiatic lions

Table 1. Comparison of welfare indices between captive-born and wild-rescued Asiatic lions

Life-histories	**Captive-born**	**Wild-rescued**	**t(33)**	**p-value**	**Effect size (Cohen's d)**
Enclosure usage	0.47±0.12	0.67±0.15	4.28	<0.000	1.47
Behaviour diversity	1.26±0.3	0.83±0.35	-3.94	<0.00	1.35
Aberrant behaviours	7.74±5.3	13.12±6.25	2.71	0.10	0.92
Latency to novel object	18.61±21.55	72.30±48.7	4.08	<0.000	1.42
Personality	***Bold***	***Shy***	**t(33)**	**p-value**	***Effect size (Cohen's d)***
Enclosure usage	0.5±0.12	0.71±0.15	-4.572	<0.000	1.54
Behaviour diversity	1.23±0.26	0.73±0.34	4.897	<0.000	1.64
Aberrant behaviours	7.01±3.9	16.13±5.4	-5.825	<0.000	1.94
Latency to novel object	11.13± 3.65	102.71±17.4	-1.11	<0.000	7.28
Sex	***Male***	***Female***	**t(33)**	**p-value**	***Effect size (Cohen's d)***
Enclosure usage	0.61±0.2	0.57±0.15	5.28	0.60	0.17
Behaviour diversity	0.96±0.43	1.1±0.35	-0.85	0.4	0.28
Aberrant behaviours	11.04±7.05	10.41±6.02	0.282	0.78	0.09
Latency to novel object	37.02±45	54.91±47.8	-1.11	0.27	0.38

Table 2(on next page)

Correlations between welfare indices and life history parameters

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1 Table 1. Correlations between welfare indices and life history parameters

	Enclosure usage	*Behaviour diversity*	*Aberrant behaviours*	*Latency to novel object*	*Age*
Enclosure usage					
Behaviour diversity	-0.611**				
Aberrant behaviours	0.536**	-0.884**			
Latency to novel object	0.593**	-0.587**	0.569**		
Age	0.261	0.127	-0.240	-0.085	

2 ** $p < 0.01$, * $p < 0.05$
3

Table 3 (on next page)

General linear regression results for inter-relationships between welfare measures

Table 3. General linear regression results for inter-relationships between welfare measures

Independent variables	Estimates	Std error	t	p values	R-squared	F	Durbin-Watson
Enclosure usage							
(Intercept)	8.22e-01	6.56e-02	12.52	7.09e-14	0.66	20.66	1.9
Age	-3.46e-05	1.35e-05	2.56	.0152			
Latency to novel objects	1.31e-03	5.10e-04	2.56	0.01			
Behaviour diversity	-3.25e-01	5.03e-02	-6.47	2.79e-07			
Behaviour diversity							
(Intercept)	1.793	0.09	18.870	2e-16	0.85	90.92	1.78
Enclosure space usage	-0.459	0.20	-2.258	0.030			
Aberrant repetitive behaviour	-0.046	0.005	-8.49	1.04e-09			
Aberrant repetitive behaviour							
Intercept	2.808e+01	1.494e+00	18.793	< 2e-16	0.85	90.27	1.58
Behaviour diversity	-1.505e+01	1.144e+00	-13.151	1.89e-14			
age	-6.779e-04	3.071e-04	-2.207	0.0346			

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