# Enrichment and animal age, not biological variables, predict positive welfare indicators in zoo-housed carnivores

by Ward, S.J., Hosey, G., Williams, E. and Bailey, R.



Ward, S.J., Hosey, G., Williams, E. and Bailey, R. 2023. 'Enrichment and animal age, not biological variables, predict positive welfare indicators in zoo-housed carnivores'. *Applied Animal Behaviour Science*, Article number 106006

18 July 2023

Applied Animal Behaviour Science 270 (2024) 106006

Contents lists available at ScienceDirect

Applied Animal Behaviour Science

journal homepage: www.elsevier.com/locate/applanim

# Enrichment and animal age, not biological variables, predict positive welfare indicators in zoo-housed carnivores

Samantha J. Ward [a,*,1], Geoff Hosey [b,2], Ellen Williams [c,3], Richard Bailey [d,4]

[a] School of Animal, Rural and Environmental Sciences, Nottingham Trent University, UK
[b] University of Bolton, UK
[c] Department of Animal Health, Behaviour & Welfare, Harper Adams University, UK
[d] Department of Ecology and Vertebrate Zoology, University of Łódź, Łódź, Poland

ARTICLE INFO

*Keywords:*
Captive
Phylogenetic
Activity
Play
Interaction
Behaviour
Affective state

ABSTRACT

The development of evidence-based zoo animal welfare science and the use of the 'five domains' have inspired zoos to increase animal welfare, particularly recognising positive welfare states. We tested whether natural biology (number of habitats, latitudinal range, sociality, body weight) or husbandry variables (mean age of group, group size and presence of extra enrichment) predict rates of positive welfare indicators (activity, play and engagement with the environment) in the Order Carnivora from collecting data from previously published articles. For each behaviour, species (n = 23) medians were analysed using phylogenetically informed mixed-model regression. Activity data were from 136 animals (n = 23 species), environmental interaction from 55 animals (n = 15 species) and play from 27 animals (n = 7 species). Biological variables did not predict rates of behaviour at a species or an individual animal level, but husbandry variables did. At an individual level, activity and play decreased in older animals. Activity and interaction with environment also increased with additional enrichment. This study is the first to quantify positive behaviours performed by zoo housed Carnivora and shows that they display indicators of positive welfare, if appropriate husbandry including environmental enrichment is provided.

## 1. Introduction

Zoo animal welfare research is increasing in both number (Binding et al., 2020) and importance, with an increased focus on the advancement of evidence-based animal management decisions that will support sustainable captive populations across zoos worldwide (Ward and Hosey, 2019). In previous years, a high proportion of research has shown that animals in zoos are not in self-sustaining populations (Barnes et al., 2002; Snyder et al., 1996). Issues such as poor conception rates, high infant mortality rates, and/or poor adult survivorship have been reported in a range of scientific articles (Clubb and Mason, 2007). Furthermore, abnormal behaviours such as repetitive pacing and other stereotypies, that likely reflect the provision of inadequate environments at some point in the animal's history, are perceived negatively by the public, and could even indicate psychological changes that could impede reintroduction success (Mason et al., 2007).

For a number of megafauna housed in zoos, including Carnivora, zoo animal welfare research needs to move beyond identifying negative welfare indicators (and subsequent assumptions that an absence of poor welfare equates to good welfare) and focus more on the achievement and assessment of positive welfare outcomes. Advances in evidence-based animal management techniques (Brereton and Rose, 2022) and the use of the five domains models (Mellor, 2016; Mellor et al., 2020) to develop animal welfare assessments in zoos (EAZA, 2023; WAZA, 2023) now focus on a positive outlook, and how zoos can promote good welfare, including increasing an animal's positive mental state. The need to assess the ability of zoo animals to thrive in zoo environments has been highlighted (Ward et al., 2020). However, whilst welfare assessments

* Corresponding author.
*E-mail address:* samantha.ward@ntu.ac.uk (S.J. Ward).
1 ORCID ID: 0000-0002-5857-1071
2 ORCID ID: 0000-0002-5403-5757
3 ORCID ID: 0000-0003-4492-1605
4 ORCID ID: 0000-0001-9870-410X

https://doi.org/10.1016/j.applanim.2023.106006
Received 19 May 2023; Received in revised form 11 July 2023; Accepted 17 July 2023
Available online 18 July 2023

include the use of both positive and negative indicators of welfare and should incorporate a suite of related measures (Hill and Broom, 2009), measuring positive welfare and identifying indicators for positive mental states in multiple species is difficult and has not been completed in zoos across a wide range of species.

Difficulties arise due to our current lack of knowledge of positive behavioural indicators of wild species. For negative indicators, selecting behaviours that do not occur in the wild is a straightforward task, which is why the focus in this area has included abnormal behaviours such as stereotypies (Clubb and Mason, 2007). Additionally, positive welfare indicators in the wild are unlikely to be as straightforward; for example, is a positive behaviour a specific behaviour? A pattern of behaviour? The time spent performing specific behaviours or a combination of the above? Furthermore, behaviours shown in the wild that appear to be positive may not always be so, as we do not necessarily understand the motivations of the animals involved (Dawkins, 2023). However, what we can do is make inferences from more systematically studied species within the agricultural or laboratory welfare sciences (Ward and Hosey, 2019) where validated indicators have been identified (e.g., sheep, Zufferey et al., 2021) or other areas of zoo animal science that focuses on improving welfare in zoos more generally (Whitham and Wielebnowski, 2009). As a morphologically diverse order with a wide-ranging natural history and behavioural needs as well as known historic difficulties with captive housed species, Carnivora are a good order on which to initiate this type of research.

At a species level, positive indicators of welfare usually incorporate behavioural aspects that show comfort in (e.g. resting) or engagement with aspects of the physical and social environment (e.g. interaction with the environment, activity, or interaction with conspecifics). Positive indicators of welfare often incorporate measures that could be identified as 'species typical' (e.g. natural or functional behaviour) or those that are indicative of positive affective states (e.g. cognitive bias). Interaction with the environment has been identified as an important aspect of animal agency, which contributes to affective experiences, biological coping mechanisms and development of species typical behaviour or naturalness (Špinka, 2019). Whilst behavioural diversity has also been identified as a potential positive welfare indicator (Miller et al., 2020), others have urged caution with the use of this indicator and recommended instead focusing on validated welfare measures that are known to be sensitive to animal experiences and are appropriate for the welfare assessment being undertaken (Cronin and Ross, 2019; Watters et al., 2021).

Indicators of welfare state must be reliably measured and valid, in terms of the individual animal at that given time and over a period of time (Williams et al., 2018). As there is a paucity of validated positive indicators of welfare which can be applied to Carnivora, choosing relatively unambiguous metrics that are reasonably widely reported and that suggest active participation and engagement with the physical and social environment is important. This study assessed the impact of biological and husbandry related variables on the rate of performance of three positive welfare indicators (engagement with the environment, activity and play) in the Order Carnivora, and attempts to understand what this means in terms of likelihood of positive welfare within managed environments. The three welfare indicators meet the criteria of content validity (i.e. they have been identified as being indicative of positive welfare states) (Meagher, 2009) and therefore are beneficial in terms of understanding positive animal experiences in relation to biological and husbandry factors.

## 2. Methods

### 2.1. The database

We constructed databases containing data on three behaviours commonly used as indicators of positive welfare (activity, play and interaction with the environment), and also data on four biological variables, and three husbandry variables.

We expressed the data for the three behaviours as percentage of time spent by animals in those activities. We considered activity to be periods when the animal was not resting or asleep, but we excluded periods when the animal was engaged in pacing or other stereotypic activity. Where it was unclear how the authors of papers defined activity, those data were not used. Play was considered to include both object play and social play. Data were gained from papers in peer-reviewed journals, scientific reports and postgraduate dissertations (SM1, SM2, SM3). We found these sources through literature searches on Web of Science and Google Scholar. Search terms used were the scientific name of the species or genus AND captiv* OR zoo AND welfare OR behavio*, searching for these in the title or abstract. Behavioural data in these sources was gained from tables, from the text, or was transcribed from graphs. Data were expressed in the sources in different ways, and we converted all data, where possible, to mean percentages of time using data/figures provided by the authors, as this was the measure most authors used. In a large number of papers no descriptive data were given, or else the data could not be converted to percentages, and these sources were discarded.

We only tested biological predictor variables with values for all species in the final dataset, which therefore excluded home range size and territoriality among others. We obtained full datasets for four biological variables (latitudinal range, number of habitats occupied, whether a species was social or solitary, and species mean body weight) from the IUCN red list for each species (IUCN, 2023), using the IUCN habitat categories, and from standard mammalogical reference works (Nowack, 1991; Wilson and Mittermeier, 2009). The number of habitats listed on the IUCN red list is linked to whether the species is more of a specialist (found in a low number of different habitats) or generalist (found in a high number of different habitats) (Kroshko et al., 2016). Where any of these data were unavailable for a species, that species was excluded from the database. Husbandry data from the literature sources were mean age of group (or age of animal if it was singly housed: this was included as we anticipated that age would strongly influence play behaviour), number of animals in the group and whether additional enrichment was being provided. The rationale for the latter was that in most studies the animals lived in enclosures which as a matter of routine were enriched in some way, but a large proportion of studies were reports of the provision of additional enrichment, and provided both baseline (before enrichment) and enriched (after provision of enrichment) behavioural data.

The form of results reported in the different literature sources was variable, with some authors reporting data for individual animals and others providing pooled data for a group of animals. In many papers some of the husbandry data we sought were missing, which resulted in some studies being excluded from analysis. Consequently, we constructed two databases, one with individual data and one with group data. From these we produced a third database of median levels of each behaviour for each species, as recommended for this type of study (Spiegelhalter et al., 2002). The database for activity contained data for 136 individuals of 23 different species (SM1), the database for interaction with environment contained 55 individuals of 15 species (SM2), and the play database contained 27 individuals of 7 species (SM3).

### 2.2. Data analysis

Analyses were undertaken to determine if any of our independent variables (biological or husbandry) significantly predicted our dependent variables (percentage of time spent in activity, interaction with the environment, or play). We used phylogenetically controlled Bayesian linear mixed-models using package "MCMCglmm" in R (Mellor et al., 2018). All analyses were run for 1 million total iterations, with a burnin of 200k and thinning of 400. Prior to analysis, percentage response values were logit transformed ((percent + 0.1)/100) to improve normality. All numerical predictors were mean-centred and scaled to unit variance.

Two sets of analyses were undertaken: (i) individual level, when data were analysed for individual studies and each individual study animal was represented by its own data set and (ii) species level, when data from all studies were summarised at a species level. Both models included phylogeny (phylogenetic tree was Carnivora, obtained from TreeBASE.org and downloaded as a.nex file, this can be read into R using the 'read.nexus' command from the 'ape' package) as a random factor to control for non-independence among data points due to evolutionary relationships. It is expected that more closely related species pairs should have more similar trait values and trait similarities become more random the more distantly related species are. Biological variables were fitted as fixed effects in species level models. Individual level analyses included location and individual as additional random effects and biological and husbandry variables as fixed effects. Location was included to control for localised differences among zoos in activity levels, or how they were measured. Individual was included to control for repeated measurements of activity for some individuals.

Models were undertaken using backwards elimination; all predictors were included in the 'full' model and least significant predictors were sequentially removed with the model rerun in between each modification, until a 'final' model was reached which included only potentially important predictors. The Deviance Information Criterion (DIC) (Spiegelhalter et al., 2002) was used to ensure that removing predictors did not significantly reduce overall model fit. The aim of the backwards elimination method was to identify a model in which the most amount of variation in animal activity was explained using the smallest number of predictor variables. During each model modification it was ensured that DIC value did not increase by > 1 in comparison to the 'full' model, thereby ensuring removal of the variable did not significantly reduce the fit of the model. Final models are reported in the results. See SM4 for R Code.

## 3. Results

### 3.1. Individual level analysis

The results of this analysis are shown in Table 1. None of the biological variables significantly predicted activity, play or interaction with the environment ($p > 0.05$). Positive indicators of welfare were only affected by husbandry variables. Activity is predicted by the mean age of the social group (mean, 95%CI) (−0.19, −0.35 to −0.01, $p = 0.03$) and the presence of additional enrichment (−0.64, −0.94 to −0.39, $p = 0.0005$). As the mean age of the group increases, activity decreases (Fig. 1). Activity and interaction with the environment (−2.11, −3.03 to −1.11, $p = 0.0005$) are significantly greater when additional enrichment is provided, compared to baseline conditions (Figs. 2 and 4). Play is also significantly predicted by group age (−0.90, −1.45 to −0.31, $p = 0.003$), such that as group age increases, play decreases (Fig. 3).

### 3.2. Species level analysis

Analysis of the species medians generated the results shown in Table 2. Only biological variables were included as predictors in this analysis, and none of them significantly predicted the three behaviours ($p > 0.05$).

## 4. Discussion

Activity, play and interaction with the environment, which are all considered to be measures of positive welfare, are not predicted by biological variables (latitudinal range, number of habitats, sociality and mean body weight), but are predicted by mean age of the social group and presence of environmental enrichment. This suggests that there may be no intrinsic reason why any species of carnivore should not experience positive welfare when zoo-housed, and, further, that provision of appropriate husbandry should be able to provide a captive environment which is amenable to good welfare for any member of this order. It is important to mention that welfare is measured on a continuum scale and data collected within all of the studies utilised for this research are a snapshot of what that animal was experiencing across the timeframe of data collection. Additionally, if researchers aim to identify negative, or in this case, positive welfare indicators, the focus can create a bias towards an animal's affective state in captivity rather than an overall welfare picture of whether these species are suitable for captivity or not. It is therefore crucial that future behavioural research encompasses both the positive and negative affective states that could be associated with zoo animal welfare so that a holistic view of their affective state is interpretable. If we revert back to the definition of animal welfare, it is the ability of the animal to cope physically and psychologically within a given situation. We suggest that identifying validated positive welfare indicators across different taxa is a needed step forwards in zoo animal

**Table 1**
Generalized linear mixed model results for fixed effect predictors against logit (proportion behaviour) for the individuals level dataset. "CI" = 95% credible intervals. All numerical variables were centred and scaled prior to analysis. GLMMs were run with the following as reference levels: (1) Environmental enrichment, status 'enriched'; (2) Social, status 'not social'.

| Response | Predictor | DIC | Posterior mean and CI | p value |
|---|---|---|---|---|
| Overall activity | Intercept | 488.68 | -0.16 (−1.12, 0.90) | 0.69 |
| | Latitudinal range | | -0.03 (−0.40, 0.34) | 0.90 |
| | N habitats | | -0.31 (−0.66, 0.02) | **0.09** |
| | Social Y/N | | -0.46 (−1.46, 0.36) | 0.32 |
| | Mean bodyweight | | 0.05 (−0.34, 0.42) | 0.74 |
| | Group age | | -0.19 (−0.35, −0.01) | **0.03*** |
| | N individuals in group | | 0.0007 (−0.27, 0.27) | 0.98 |
| | Environmental enrichment | | -0.64 (−0.94, −0.39) | **<5e-4*** ** |
| Play | Intercept | 123.47 | -3.76 (−24.66, 16.66) | 0.45 |
| | Latitudinal range | | -1.51 (−15.64, 14.15) | 0.67 |
| | N habitats | | 1.61 (−4.70, 8.29) | 0.35 |
| | Social Y/N | | -1.94 (−38.79, 26.74) | 0.70 |
| | Mean bodyweight | | -0.08 (−14.01, 12.13) | 0.95 |
| | Group age | | -0.90 (−1.45, −0.31) | **0.003**** |
| | N individuals in group | | 1.22 (−1.02, 3.54) | 0.26 |
| | Environmental enrichment | | 0.57 (−0.52, 1.71) | 0.29 |
| Interaction with environment | Intercept | 258.36 | -2.62 (−5.98, 0.79) | 0.10 |
| | Latitudinal range | | -0.51 (−2.63, 1.16) | 0.66 |
| | N habitats | | 0.25 (−1.05, 1.55) | 0.73 |
| | Social Y/N | | -0.14 (−3.16, 3.14) | 0.96 |
| | Mean bodyweight | | -0.16 (−1.33, 1.02) | 0.72 |
| | Group age | | -0.31 (−0.75, 0.13) | 0.18 |
| | N individuals in group | | 0.30 (−0.48, 0.97) | 0.44 |
| | Environmental enrichment | | -2.11 (−3.03, −1.11) | **<5e-4*** ** |

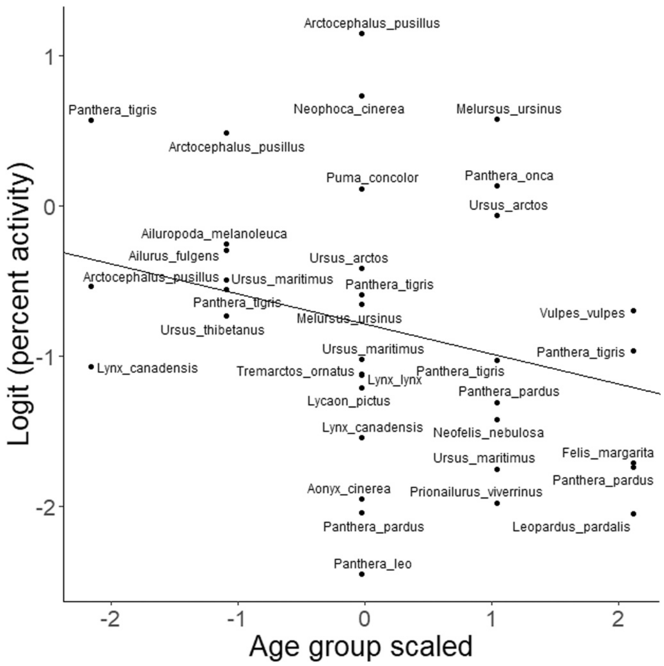


**Fig. 1.** Fitted regression line of logit(proportion activity) against group age category scaled to unit variance, from an individual-level analysis with no other fixed effect predictors and individual, group, and the phylogeny included as random effects. Points (species names) are species means by age group, jittered slightly to reduce overlap.

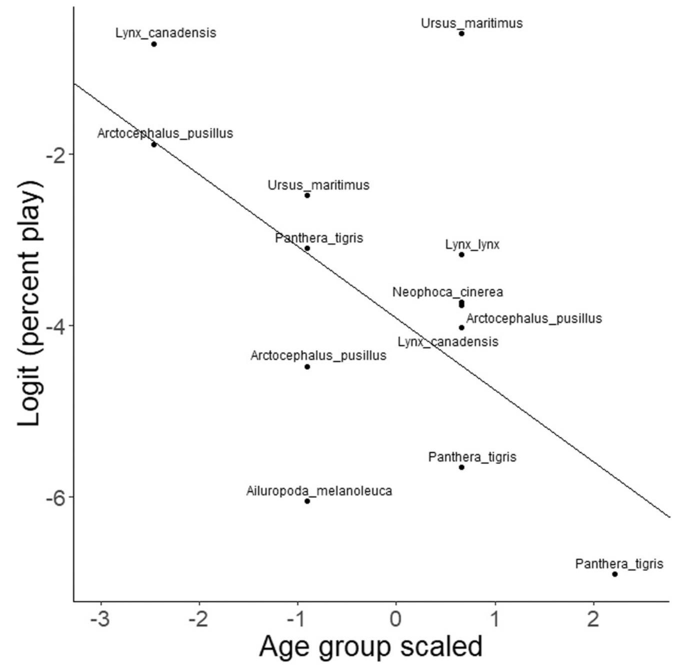


**Fig. 3.** Fitted regression line of logit(proportion play) against group age category scaled to unit variance, from an individual-level analysis with no other fixed effect predictors and individual, group, and the phylogeny included as random effects. Points (species names) are species means by age group, jittered slightly to reduce overlap.

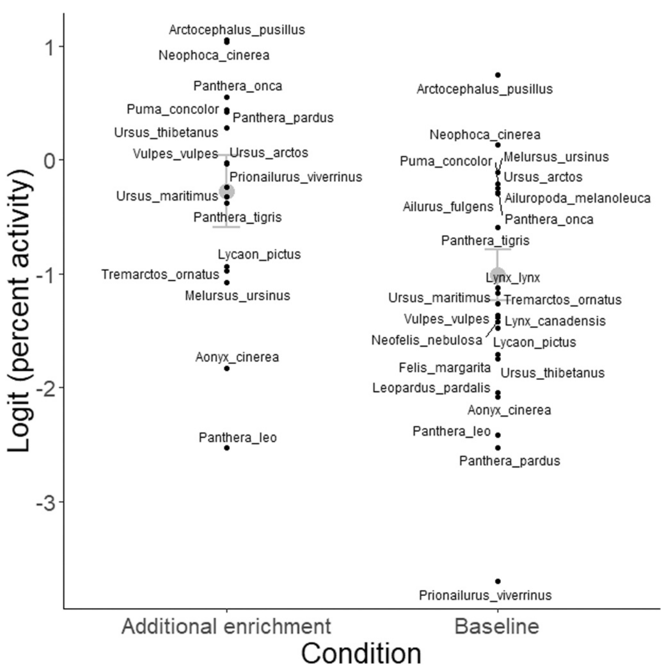


**Fig. 2.** Mean and 95% confidence intervals (grey points and error bars) for logit(proportion activity) against baseline versus enriched zoo conditions, with species means (species names) per condition.

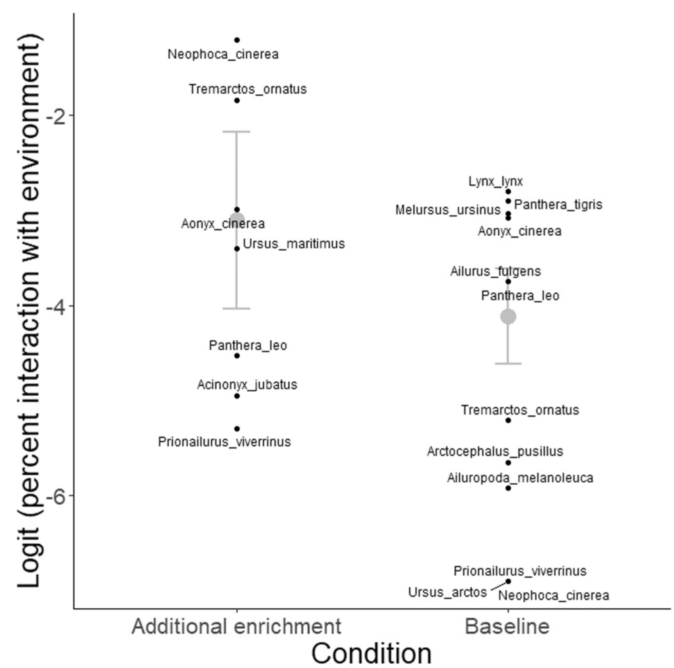


**Fig. 4.** Mean and 95% confidence intervals (grey points and error bars) for logit(proportion interaction with environment) against baseline versus enriched zoo conditions, with species means (species names) per condition.

welfare research and that future work would be to focus on a welfare roadmap to track net gain in welfare state. This positive change in welfare is likely to impact more prominently on an animals' mental states, and thus contribute to the overall welfare experienced by the animal (Mellor et al., 2020).

Members of Carnivora are often seen as challenging to maintain with good welfare in zoos, as they appear to be susceptible to developing stereotypies such as pacing, and some species show poor reproduction in captivity (Clubb and Mason, 2007; Hunt, 2022). For this reason, a great deal of the welfare-related research undertaken on zoo-housed carnivores has been concerned with understanding the causes and correlates of stereotypies, particularly in felids and ursids (Mallapur, 2002; Burgener et al., 2008; Fernandez, 2021; Vickery and Mason, 2004; Bashaw et al., 2007; Bauer et al., 2013; Cremers and Geutjes, 2012 and Wechsler,

**Table 2**
Generalized linear mixed model results for fixed effect predictors against logit (proportion behaviour) for the species level dataset. "CI" = 95% credible intervals. All numerical variables were centred and scaled prior to analysis. GLMMs were run with the following as reference levels: (1) Environmental enrichment, status 'enriched'; (2) Social, status 'not social'.

| Response | Predictor | DIC | Posterior mean and CI | p value |
|---|---|---|---|---|
| Overall activity | Intercept | 74.77 | -0.79 (−1.76, 0.47) | 0.15 |
| | Latitudinal range | | -0.06 (−0.42, 0.33) | 0.77 |
| | N habitats | | -0.06 (−0.45, 0.31) | 0.74 |
| | Social Y/N | | -0.16 (−1.27, 0.95) | 0.79 |
| | Mean bodyweight | | 0.04 (−0.38, 0.44) | 0.87 |
| Play | Intercept | 0.16 | -3.59 (−7.81, 0.04) | 0.06 |
| | Latitudinal range | | -0.81 (−3.60, 1.73) | 0.48 |
| | N habitats | | 0.79 (−1.34, 2.78) | 0.36 |
| | Social Y/N | | -0.39 (−3.61, 2.82) | 0.78 |
| | Mean bodyweight | | 0.28 (−2.11, 2.73) | 0.78 |
| Interaction with environment | Intercept | 70.1 | -3.92 (−5.90, −2.12) | 0.01 |
| | Latitudinal range | | -0.26 (−1.41, 0.98) | 0.65 |
| | N habitats | | 0.18 (−0.93, 1.22) | 0.72 |
| | Social Y/N | | 0.84 (−1.29, 3.16) | 0.41 |
| | Mean bodyweight | | -0.45 (−1.48, 0.71) | 0.37 |

1991). Studies using comparative analysis, have shown that locomotory stereotypies in zoo-housed carnivores are predicted by aspects of the natural biology of different species, notably their ranging behaviour (Clubb and Mason, 2007; Cremers and Geutjes, 2012 and Clubb and Vickery, 2006). Based on these studies, they suggest that some species of Carnivora (and indeed of other orders: Mason, 2010) were perhaps unsuitable for captivity and should not be held in zoos. However, zoos have shown significant advancements in welfare provisioning in recent years and recognise the need for monitoring and improving welfare (WAZA, 2023). For order Carnivora it is imperative that the ability to cater for these species in zoos is reassessed using positive metrics, in addition to previous negative indicators, thus providing a more holistic overview of the viability of zoos in relation to positive welfare for Carnivora. There is a pressing need for conservation of carnivores (Gittleman et al., 2001) and for some species, captive breeding in zoos contributes to that (Santymire, 2019).

The provision of environmental enrichment can significantly reduce the incidence of stereotypies (Swaisgood and Shepherdson, 2005; Shyne, 2006), so being at risk from natural biology need not be an impediment to experiencing good welfare in zoos. Our analysis shows that enrichment is not just important in reducing stereotypies but is a significant predictor for activity and interaction with the environment. Both measures were higher in groups who received additional enrichment compared to those at baseline levels. Indeed, the aim of enrichment is often stated to be to increase activity, not just to decrease stereotypies (e.g. Kistler et al., 2009; Cloutier and Packard, 2014). Interaction with the environment is an important aspect of animal agency, which is essential in good welfare for managed animals (Whitham and Wielebnowski, 2009). Providing environments which enable and encourage animals to be active and engaged with their environments are therefore beneficial to positive welfare. This in turn implies that we can offer the animals the choice to do something they want to do, which is a much more appropriate measure of positive welfare than simply looking to see how 'natural' their behaviour looks (Dawkins, 2023).

The other significant predictor of our welfare variables was the mean age of the group, such that as mean age increased, both activity and play decreased. Neither of these are surprising. As mammals age they generally show a decline in overall activity levels, across all orders (Krebs et al., 2018). Play is typically associated with young animals and is seen less frequently in adults. In domestic cats, object play appears to be linked to predation and can be elicited by objects which have prey-like stimuli (Hall, 1998), suggesting that enrichment with such objects can help promote behaviours associated with predatory behaviours that zoo-housed carnivores are unable to otherwise show.

The failure of biological variables to predict any of our measures of positive welfare is surprising. Mason (2010) had suggested that the features of 'weed species' (species that thrive in human-disturbed habitats and may also be successfully invasive) may help us understand what natural characteristics may predispose certain species to cope within a zoo environment. These characteristics include boldness, behavioural flexibility and not being migratory, and are associated with generalist rather than specialist species. In a study of 80 individual zoo-housed carnivores representing 34 different species, Miller et al. (2019) found that generalist species showed higher behavioural diversity, which is a possible measure of positive welfare (Miller et al., 2020) and offspring production compared to specialist species. In our analysis we used latitudinal range and number of habitats occupied in the wild as measures of ecological and behavioural flexibility, and hence of generalist species, but neither significantly predicted our three measures of positive welfare. Number of habitats came close to significance ($p = 0.09$) for predicting activity, so it is possible that with a larger database in future this might become a significant predictor.

Our results provide a strong message about the effectiveness of environmental enrichment not only in reducing negative or unwanted behaviours in zoo-housed carnivores, but also in promoting positive behaviours. Results also suggest we should be cautious of relying too heavily on activity and play as indicators of positive welfare, as both show a decline as animals age. In addition, activity is likely contextual and could vary according to time of day or the time since last eating in the case of Carnivora, for example. More studies are needed using other measures of positive welfare, such as behavioural variety, anticipatory behaviour, interaction with humans and cognitive bias (Ward and Hosey, 2019; Miller et al., 2020; Wolfensohn et al., 2018; Whitham and Wielebnowski, 2013). At the moment there are too few data using any of these measures in carnivores to be able to undertake the kind of analysis we have done here.

### *4.1. Limitations and future directions*

The welfare indicators used in this study (activity, play and engagement with the environment) met the criteria for content validity (Williams et al., 2018; Meagher, 2009). Whilst positive welfare indicators have been advocated, there is a paucity of research on positive welfare indicators in the Order Carnivora. The indicators chosen were representative of natural behaviour and were indicators that have been identified as positive indicators in other species. Furthermore, they reached a threshold in terms of the frequency of occurrence in the literature which enabled them to be investigated in relation to husbandry and biological variables. In order to further advance this work, it is important to focus on ensuring research is undertaken which enables construct and criterion validity status to be reached for a selection of welfare indicators (Williams et al., 2018; Meagher, 2009). More targeted research on a range of carnivores in different welfare states or comparing these welfare indicators to validated measures of affective state (e.g., cognitive bias, qualitative behavioural assessment) within the same animals will enable advancement of this field.

Comparative analysis, controlling for phylogeny, is a powerful method for identifying the significant predictors of animal behaviour, particularly when some of those predictors are the naturally evolved characteristics of the animals (Mellor et al., 2018). It offers the possibility of making predictions about which species might, and which species might not, thrive in captivity (Mason, 2010). The method does, however, require a lot of data. For species-level analysis of pacing behaviour, Clubb and Mason (2007) had to include species for which only one or two records were available, on the grounds that the loss of statistical power resulting from this was more acceptable than the loss of accuracy from poorly represented species. Nine years later, with more data, they were able to impose a much stricter criterion of only including a species if stereotyping data were available for at least five individuals (Kroshko et al., 2016). Despite an extensive literature search, in our study, only 23 species passed this stricter criterion for activity, and fewer for the other two measures, so we also had to relax the criteria and hence sacrifice statistical power. None of the biological predictors at the species level was statistically significant. We therefore need many more studies on a range of different carnivores, particularly those which are not big cats, polar bears (*Ursus maritimus*) or giant pandas (*Ailuropoda melanoleuca*).

The data set at an individual animal level was much larger and yielded greater statistical power. However, there were still limitations caused by the quality and quantity of data provided in the Results sections of papers. There is an unfortunate trend of authors only reporting the outcomes of inferential statistics (e.g. correlation coefficients, $\chi^2$ values, F values), and not the descriptive data (e.g. means, medians, percentages) upon which comparative analysis depends. Furthermore, even basic husbandry information such as the ages of animals or the size of their enclosure are often missing from the reported Methods sections. The importance of assessing animal behaviour on an individual basis owing to their differential experiences of managed environments and thus different welfare experiences (Watters et al., 2017) has been recognised. In addition, it is likely that the publication bias for significant results may impact on the enrichment-related findings. We therefore urge authors of studies on the behaviour and welfare of zoo-housed animals to aim to gather data at the most detailed level (e.g. an individual level where possible), always make the descriptive or summarised data available within the published paper or associated with open-access databases, to include as much basic husbandry information as possible and to publish non-significant results, and request journals and reviewers to ask for these to be included and to consider papers giving non-significant results. This will enable large-scale exploratory analysis such as undertaken here to be feasible. This is important in the development of predictive models which will help to advance zoo animal welfare on a large scale.

## 5. Conclusions

Natural biology of carnivores appears to predict the occurrence of negative welfare indicators, but this research found that the same was not true for indicators of positive welfare. Biological variables did not predict the rate of activity, interaction with the environment or play (social and object) at either a species or an individual level. At an individual level however, zoo-based husbandry variables did significantly affect the frequency of behaviour that we allocated as indicators or positive welfare. Activity and play decreased in older animals. Activity and interaction with the environment increased in the presence of additional enrichment. The results of this study highlight the fact that Carnivora can be in zoological collections and display indicators of positive welfare, if the appropriate husbandry is provided. They further emphasise the importance of environmental enrichment in optimising animal welfare. It is advocated that further, detailed studies are undertaken both at a species level and an individual level, to enable wider investigation of these concepts as well as identifying other species/ taxonomic relevant positive welfare indicators to help focus on tracking a net gain in welfare.

## Author contributions

Project conception – SW & GH. Project Design – SW, GH & EW. Acquisition of data – SW & GH. Data Analysis – RB. Interpretation of data – SW, GH, EW & RB. Article draft – SW, GH, EW & RB.

## Declaration of Competing Interest

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

## Acknowledgments

Authors wish to thank the dedicated students from Nottingham Trent University who helped to collect data for this project during the pandemic. They should have been out enjoying their work placements but COVID-19 had a different plan for them. Thanks goes to Zoe Lloyd-Davis, Leonarda Hrvanovic, Ryan Delderfield, Ana Goncalves Ferreira, Louis Hague, Charle Doran, Kira Botley and Alex McClatchie, we hope this project provided you with some positive welfare during a challenging time.

## Appendix A. Supporting information

Supplementary data tables (SM1, SM2 and SM3) associated with this article can be found in the online version at doi:10.1016/j.applanim.2023.106006.

## References

Barnes, R., Greene, K., Holland, J., Lamm, M., 2002. Management and husbandry of duikers at the Los Angeles Zoo. Zoo Biol. 21 (2), 107–121. https://doi.org/10.1002/ZOO.10020.

Bashaw, M.J., Kelling, A.S., Bloomsmith, M.A., Maple, T.L., 2007. Environmental effects on the behavior of zoo-housed lions and tigers, with a case study of the effects of a visual barrier on pacing. J. Appl. Anim. Welf. Sci. 10, 95–109. https://doi.org/10.1080/10888700701313116.

Bauer, E., Babitz, M., Boedeker, N., Hellmuth, H., 2013. Approaches to understanding and managing pacing in sloth bears in a zoological setting. Int. J. Comp. Psychol. 26, 53–74.

Binding, S., Farmer, H., Krusin, L., Cronin, K., 2020. Status of animal welfare research in zoos and aquariums: where are we, where to next? J. Zoo Aquar. Res. 8 (3), 166–174. https://doi.org/10.19227/JZAR.V8I3.505.

Brereton, J., Rose, P., 2022. An evaluation of the role of “biological evidence” in zoo and aquarium enrichment practices. Anim. Welf. 31 (1), 13–26. https://doi.org/10.7120/09627286.31.1.002.

Burgener, L., Gusset, M., Schmid, H., 2008. Frustrated appetitive foraging behavior, stereotypic pacing, and fecal glucocorticoid levels in snow leopards (Uncia uncia) in the Zurich Zoo. J. Appl. Anim. Welf. Sci. 11, 74–83. https://doi.org/10.1080/10888700701729254.

Cloutier, T.L., Packard, J.M., 2014. Enrichment options for African painted dogs (Lycaon pictus). Zoo Biol. 33, 475–480. https://doi.org/10.1002/zoo.21155.

Clubb, R., Vickery, S., 2006. Locomotory stereotypies in carnivores: does pacing stem from hunting, ranging or frustrated escape? In: Mason, G., Rushen, J. (Eds.), Stereotypic Animal Behaviour: Fundamentals and Application to Welfare, second ed. CABI, Wallingford, pp. 58–85.

Clubb, R., Mason, G.J., 2007. Natural behavioural biology as a risk factor in carnivore welfare: how analysing species differences could help zoos improve enclosures. Appl. Anim. Behav. Sci. 102 (3–4), 303–328. https://doi.org/10.1016/J.APPLANIM.2006.05.033.

Cremers, P.W.F.H., Geutjes, S.L., 2012. The cause of stereotypic behaviour in a male polar bear (Ursus maritimus). In: Spink, A.J., Grieco, F., Krips, O.E., Loijens, L.W.S., Noldus, L.P.J.J., Zimmerman, P.H. (Eds.), Proceedings of Measuring Behavior 2012 (Utrecht, The Netherlands, August 28–31, 2012) 340 (Abstract).

Cronin, K.A., Ross, S.R., 2019. Technical contribution: a cautionary note on the use of behavioural diversity (H-Index) in animal welfare science. Anim. Welf. 28 (2), 157–164. https://doi.org/10.7120/09627286.28.2.157.

Dawkins, M.S., 2023. Natural behaviour is not enough: farm animal welfare needs modern answers to Tinbergen's four questions. Animals 13 (6), 988. https://doi.org/10.3390/ani13060988.

EAZA, 2023. Animal Welfare - EAZA. ⟨https://www.eaza.net/about-us/areas-of-activity/animal-welfare/⟩.

Fernandez, E.J., 2021. Appetitive search behaviors and stereotypies in polar bears (Ursus maritimus). Behav. Process. 182, 104299 https://doi.org/10.1016/j.beproc.2020.104299.
Gittleman, J.L., Funk, S.L., Macdonald, D.W., Wayne, R.K., 2001. Why 'carnivore conservation'? In: Gittleman, J.L., Funk, S.L., Macdonald, D.W., Wayne, R.K. (Eds.), Carnivore Conservation. Cambridge University Press, pp. 1–7.
Hall, S.L., 1998. Object play by adult animals. In: Bekoff, M., Byers, J.A. (Eds.), Animal Play: Evolutionary, Comparative, and Ecological Perspectives. Cambridge University Press, pp. 45–60.
Hill, S.P., Broom, D.M., 2009. Measuring zoo animal welfare: theory and practice. Zoo Biol. 28 (6), 531–544. https://doi.org/10.1002/ZOO.20276.
Hunt, K.A., 2022. The behavioural biology of carnivores. In: Rose, P. (Ed.), The Behavioural Biology of Zoo Animals. CRC Press, Boca Raton, pp. 83–95.
IUCN, 2023. IUCN Red List of Threatened Species. 〈https://www.iucnredlist.org/〉.
Kistler, C., Hegglin, D., Würbel, H., König, B., 2009. Feeding enrichment in an opportunistic carnivore: the red fox. Appl. Anim. Behav. Sci. 116, 260–265. https://doi.org/10.1016/j.applanim.2008.09.004.
Krebs, B.L., Marrin, D., Phelps, A., Krol, L., Watters, J.V., 2018. Managing aged animals in zoos to promote positive welfare: a review and future directions. Animals 8 (7), 116. https://doi.org/10.3390/ani8070116.
Kroshko, J., Clubb, R., Harper, L., Mellor, E., Moehrenschlager, A., Mason, G., 2016. Stereotypic route tracing in captive Carnivora is predicted by species-typical home range sizes and hunting styles. Anim. Behav. 117, 197–209. https://doi.org/10.1016/j.anbehav.2016.05.010.
Mason, G., Clubb, R., Latham, N., Vickery, S., 2007. Why and how should we use environmental enrichment to tackle stereotypic behaviour? Appl. Anim. Behav. Sci. 102 (3–4), 163–188. https://doi.org/10.1016/J.APPLANIM.2006.05.041.
Mason, G.J., 2010. Species differences in responses to captivity: stress, welfare and the comparative method. Trends Ecol. Evol. 25, 713–721. https://doi.org/10.1016/j.tree.2010.08.011.
Meagher, R.K., 2009. Observer ratings: validity and value as a tool for animal welfare research. Appl. Anim. Behav. Sci. 119 (1–2), 1–14. https://doi.org/10.1016/J.APPLANIM.2009.02.026.
Mellor, D.J., 2016. Moving beyond the "Five freedoms" by updating the "five provisions" and introducing aligned "animal welfare aims. Animals 6 (10). https://doi.org/10.3390/ANI6100059.
Mellor, D.J., Beausoleil, N.J., Littlewood, K.E., McLean, A.N., McGreevy, P.D., Jones, B., Wilkins, C., 2020. The 2020 five domains model: including human–animal interactions in assessments of animal welfare. Animals 10 (10), 1–24. https://doi.org/10.3390/ANI10101870.
Mellor, E., McDonald Kinkaid, H., Mason, G., 2018. Phylogenetic comparative methods: harnessing the power of species diversity to investigate welfare issues in captive wild animals. Zoo Biol. 37 (5), 369–388. https://doi.org/10.1002/ZOO.21427.
Miller, L.J., Vicino, G.A., Sheftel, J., Lauderdale, L.K., 2020. Behavioral diversity as a potential indicator of positive animal welfare. Animals 10, 1211. https://doi.org/10.3390/ANI10071211.
Miller, L.J., Ivy, J.A., Vicino, G.A., Schork, I.G., 2019. Impacts of natural history and exhibit factors on carnivore welfare. J. Appl. Anim. Welf. Sci. 22, 188–196. https://doi.org/10.1080/10888705.2018.1455582.
Nowack, R.M., 1991. Walker's Mammals of the World, fifth ed. Johns Hopkins University Press.
Santymire, R., 2019. Saving the black-footed ferret from extinction: in theory and practice. In: Kaufman, A.B., Bashaw, M.J., Maple, T.L. (Eds.), Scientific Foundations of Zoos and Aquariums: Their Role in Conservation and Research. Cambridge University Press, pp. 440–473.
Shyne, A., 2006. Meta-analytic review of the effects of enrichment on stereotypic behavior in zoo mammals. Zoo Biol. 25, 317–337. DOI 10.1002/zoo.20091.
Snyder, N.F.R., Derrickson, S.R., Beissinger, S.R., Wiley, J.W., Smith, T.B., Toone, W.D., Miller, B., 1996. Limitations of captive breeding in endangered species recovery. Conserv. Biol. 10 (2), 338–348. https://doi.org/10.1046/J.1523-1739.1996.10020338.
Spiegelhalter, D.J., Best, N.G., Carlin, B.P., Van Der Linde, A., 2002. Bayesian measures of model complexity and fit. J. R. Stat. Soc. Ser. B Stat. Methodol. 64 (4), 583–639.
Špinka, M., 2019. Animal agency, animal awareness and animal welfare. Anim. Welf. 28 (1), 11–20. https://doi.org/10.7120/09627286.28.1.011.
Swaisgood, R.R., Shepherdson, D.J., 2005. Scientific approaches to enrichment and stereotypies in zoo animals: what's been done and where should we go next? Zoo Biol. 24, 499–518. https://doi.org/10.1002/zoo.20066.
Vickery, S., Mason, G., 2004. Stereotypic behavior in Asiatic black and Malayan sun bears. Zoo Biol. 23, 409–430. https://doi.org/10.1002/zoo.20027.
Ward, S.J., Hosey, G., 2019. The need for a convergence of agricultural/laboratory and zoo-based approaches to animal welfare. J. Appl. Anim. Welf. Sci. 23 (4) https://doi.org/10.1080/10888705.2019.1678038.
Ward, S.J., Williams, E., Groves, G., Marsh, S., Morgan, D., 2020. Using zoo welfare assessments to identify common issues in developing country zoos. Animals 10, 2101. https://doi.org/10.3390/ANI10112101.
Watters, J.v., Krebs, B.L., Eschmann, C.L., Behavior, A., 2021. Assessing animal welfare with behavior: onward with caution. J. Zool. Bot. Gard. 2, 75–87. https://doi.org/10.3390/JZBG2010006.
Wechsler, B., 1991. Stereotypies in polar bears. Zoo Biol. 10 (2), 177–188.
Whitham, J.C., Wielebnowski, N., 2009. Animal-based welfare monitoring: using keeper ratings as an assessment tool. Zoo Biol. 28 (6), 545–560. https://doi.org/10.1002/ZOO.20281.
Whitham, J.C., Wielebnowski, N., 2013. New directions for zoo animal welfare science. Appl. Anim. Behav. Sci. 147, 247–260. https://doi.org/10.1016/j.applanim.2013.02.004.
Williams, E., Chadwick, C.L., Yon, L., Asher, L., 2018. A review of current indicators of welfare in captive elephants (Loxodonta africana and Elephas maximus. Anim. Welf. 27 (3), 235–249. https://doi.org/10.7120/09627286.27.3.235.
Wilson, D.E., Mittermeier, R.A., 2009. Handbook of the Mammals of the World (Carnivores, Vol. 1). Lynx Edicions.
Wolfensohn, S., Shotton, J., Bowley, H., Davies, S., Thompson, S., Justice, W.S.M., 2018. Assessment of welfare in zoo animals: towards optimum quality of life. Animals 8 (7). https://doi.org/10.3390/ani8070110.
WAZA, 2023. 2023 Animal Welfare Goal – WAZA. 〈https://www.waza.org/priorities/animal-welfare/2023-animal-welfare-goal/〉.
Zufferey, R., Minnig, A., Thomann, B., Zwygart, S., Keil, N., Schüpbach, G., Miserez, R., Zanolari, P., Stucki, D., 2021. Animal-based indicators for on-farm welfare assessment in sheep. Animals 11, 2973. https://doi.org/10.3390/ani11102973.

## Additional references used in constructing the database

Abston, M.C., 2008. Effects of Olfactory Enrichment on African Cheetahs (Acinonyx jubatus) (Masters thesis). Southern Illinois University Carbondale.
Altman, J.D., 1999. Effects of inedible, manipulable objects on captive bears. J. Appl. Anim. Welf. Sci. 2 (2), 123–132.
Antonenko, T.V., Matsyura, A.V., Pysarev, S.V., 2019a. Influence of cinnamon on the behavior of Amur tiger (Panthera tigris altaica, Temminck, 1844) in captivity. Ukr. J. Ecol. 9 (3), 332–334.
Antonenko, T.V., Ulitina, O.M., Pysarev, S.V., Matsyura, A.V., 2019b. Different enriched environments for Eurasian lynx in the Barnaul Zoo. Ukr. J. Ecol. 9 (4), 671–675.
Biolatti, C., Modesto, P., Dezzutto, D., Pera, F., Tarantola, M., Gennero, M.S., Maurella, C., Acutis, P.L., 2016. Behavioural analysis of captive tigers (Panthera tigris): a water pool makes the difference. Appl. Anim. Behav. Sci. 174, 173–180. https://doi.org/10.1016/j.applanim.2015.11.017.
Canino, W., Powell, D., 2010. Formal behavioral evaluation of enrichment programs on a zookeeper's schedule: a case study with a polar bear (Ursus maritimus) at the Bronx Zoo. Zoo Biol. 29, 503–508. DOI 10.1002/zoo.20247.
Carlsson, L., 2009. Activity and Enclosure Use of a Sand Cat in Parken Zoo, Eskilstuna (thesis). Mälardalen University.
Caudron, A.K., 1995. Social behaviour of Cape fur seals Arctocephalus pusillus pusillus in captivity. Aquat. Mamm. 21.1, 7–17.
Cederquist, H., 2021. Change in the behaviors and spatial use of Canada lynx (Lynx canadensis) over time at John Ball Zoo. Stud. Summer Sch. Manuscr. 215. 〈https://scholarworks.gvsu.edu/sss/215〉.
Dahl, F.M., Hansen, H.H., Vorup, L.D., Jensen, L.Ø., Spyridopoulos, P.S., Jensen, T.H., Pertoldi, C., Alstrup, A.K.O., Pagh, S., 2020. Effects of enrichment on behavioural reaction norms of two captive polar bears (Ursus maritimus) in Aalborg Zoo, Denmark. Genet. Biodivers. J. Spec. Issue (Behav. Instab.) 61–72.
De Rouck, M., Kitchener, A.C., Law, G., Nelissen, M., 2005. A comparative study of the influence of social housing conditions on the behaviour of captive tigers (Panthera tigris). Anim. Welf. 14, 229–238.
Dybowska, J., Górecka, J., Grzegrzólka, B., Wieczorek, M., Złamal, A., 2008. Analysis of the influence of environmental enrichment on the behaviour of wild cats kept in captivity. Annals of Warsaw University of Life Sciences – SGGW Animal Science No. 45, pp. 3–17.
Fischbacher, M., Schmid, H., 1999. Feeding enrichment and stereotypic behavior in spectacled bears. Zoo Biol. 18, 363–371.
Forthman, D.L., Elder, S.D., Bakeman, R., Kurkowski, T.W., Noble, C.C., Winslow, S.W., 1992. Effects of feeding enrichment on behavior of three species of captive bears. Zoo Biol. 11, 187–195.
Frilot, M., Medved, E., 2014. Red panda (Ailurus fulgens) behaviors and exhibit use at the Memphis Zoo. Rhodes J. Biol. Sci. 29, 51–57.
Hadfield, J.D., 2010. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. J. Stat. Softw. 33, 1–22.
Hocking, D.P., Salverson, R., Evans, A.R., 2015. Foraging-based enrichment promotes more varied behaviour in captive Australian fur seals (Arctocephalus pusillus doriferus). PLoS ONE 10 (5), e0124615. https://doi.org/10.1371/journal.pone.0124615.
Kachamakova, M., Zlatanova, D., 2014. Behaviour of Eurasian lynx, Lynx lynx (L.), in captivity during the breeding season. Acta Zool. Bulg. 66 (3), 365–371.
Kelly, K.R., Harrison, M.L., Size, D.D., MacDonald, S.E., 2015. Individual effects of seasonal changes, visitor density, and concurrent bear behavior on stereotypical behaviors in captive polar bears (Ursus maritimus). J. Appl. Anim. Welf. Sci. 18 (1), 17–31. https://doi.org/10.1080/10888705.2014.924832.
Law, G., Tatner, P., 1998. Behaviour of a captive pair of clouded leopards (Neofelis nebulosa): introduction without injury. Anim. Welf. 7, 57–76.
Leeds, A., Stone, D., Johnson, B., Less, E., Schoffner, T., Dennis, P., Lukas, K., Wark, J., 2016. Managing repetitive locomotor behaviour and time spent off exhibit in a male black-footed cat (Felis nigripes) through exhibit and husbandry modifications. J. Zoo Aquar. Res. 4 (2), 109–114.
Linder, A.C., Gottschalk, A., Lyhne, H., Langbak, M.G., Jensen, T.H., Pertoldi, C., 2020. Using behavioral instability to investigate behavioral reaction norms in captive animals: theoretical implications and future perspectives. Symmetry 2020 (12), 603. https://doi.org/10.3390/sym12040603.
Mallapur, A., Qureshi, Q., Chellam, R., 2002. Enclosure design and space utilization by Indian leopards (Panthera pardus) in four zoos in southern India. J. Appl. Anim. Welf. Sci. 5 (2), 111–124.
Markowitz, H., Aday, C., Gavazzi, A., 1995. Effectiveness of acoustic "prey": environmental enrichment for a captive African leopard (Panthera pardus). Zoo Biol. 14, 371–379.

Mishra, A.K., Guru, B.C., Patnaik, A.K., 2013. Effect of feeding enrichment on behaviour of captive tigers. Indian Zoo Yearb. 7, 124–133.

Pastorino, G.Q., Brereton, J.E., Drago, F., Mazzonetto, F., Confalonieri, E., Preziosi, R., 2021. Investigating the effect of social grouping on the behaviour of captive leopards. J. Zoo Aquar. Res. 9 (2), 116–123. https://doi.org/10.19227/jzar.v9i2.548.

Pastorino, G.Q., Christodoulides, Y., Curone, G., Pearce-Kelly, P., Faustini, M., Albertini, M., Preziosi, R., Mazzola, S.M., 2017a. Behavioural profiles of brown and sloth bears in captivity. Animals 2017 (7), 39. https://doi.org/10.3390/ani7050039.

Pastorino, G.Q., Paini, F., Williams, C.L., Faustini, M., Mazzola, S.M., 2017b. Personality and sociality in captive tigers (Panthera tigris). Annu. Res. Rev. Biol. 21 (2), 1–17.

Pastorinoc, G.Q., Viau, A., Curone, G., Pearce-Kelly, P., Faustini, M., Vigo, D., Mazzola, S. M., Preziosi, R., 2017. Role of personality in behavioral responses to new environments in captive Asiatic lions (Panthera leo persica). Vet. Med. Int. 2017, 6585380 https://doi.org/10.1155/2017/6585380.

Powell, D.M., Carlstead, K., Tarou, L.R., Brown, J.L., Monfort, S.L., 2006. Effects of construction noise on behavior and cortisol levels in a pair of captive giant pandas (Ailuropoda melanoleuca). Zoo Biol. 25 (5), 391–408. https://doi.org/10.1002/ZOO.20098.

Rafacz, M.L., Heintz, M.R., Santymire, R.M., 2016. Hormonal and behavior responses to odor cues in zoo-housed African painted dogs (Lycaon pictus). In: Schulte, B.A., Goodwin, T.E., Ferkin, M.H. (Eds.), Chemical Signals in Vertebrates 13. Springer, pp. 391–400.

Regaiolli, B., Rizzo, A., Ottolini, G., Petrazzini, M.E.M., Spiezio, C., Agrillo, C., 2019. Motion illusions as environmental enrichment for zoo animals: a preliminary investigation on lions (Panthera leo). Front. Psychol. 10, 2220. https://doi.org/10.3389/psyg.2019.02220.

Renner, M.J., Lussier, J.P., 2002. Environmental enrichment for the captive spectacled bear (Tremarctos ornatus). Pharmacol. Biochem. Behav. 73, 279–283.

Ross, S.R., 2002. The effect of a simple feeding enrichment strategy on the behavior of two Asian small-clawed otters (Aonyx cinerea). Aquat. Mamm. 28.2, 113–120.

Shepherdson, D.J., Carlstead, K., Mellen, J.D., Seidensticker, J., 1993. The influence of food presentation on the behavior of small cats in confined environments. Zoo Biol. 12 (2), 203–216.

Siahaan, D.A.S., Berliani, K., Hartanto, A., Tanjung, H.M.M., Nurbayti, 2020. Study on daily activity pattern of captive lion (Panthera leo) in Siantar Zoo, North Sumatra, Indonesia. IOP Conf. Ser. J. Phys. Conf. Ser., 1462, 012049. DOI: 10.1088/1742-6596/1462/1/012049.

Smith, B.P., Litchfield, C.A., 2010. An empirical case study examining effectiveness of environmental enrichment in two captive Australian sea lions (Neophoca cinerea). J. Appl. Anim. Welf. Sci. 13, 103–122.

Van Metter, J.E., Harriger, M.D., Bolen, R.H., 2007. Environmental enrichment utilizing stimulus objects for African lions (Panthera leo leo) and Sumatran tigers (Panthera tigris sumatrae). Bios 79 (1), 7–16.

Vanhoomissen, C., 2016. Activity Budget of Two Giant Pandas at Pairi Daiza Zoo (belgium) and the Possible Influence of Environmental Factors (Masters thesis). Ghent University.

Watters, J.V., Bremner-Harrison, S., Powell, D.M., 2017. Phenotype management: an inclusive framework for supporting individuals' contributions to conservation populations. In: Vonk, J., Weiss, A., Kuczaj, S.A. (Eds.), Personality in Nonhuman Animals. Springer International Publishing, Cham, pp. 277–294. ISBN 978–3-319–59299-2.

Weller, S.H., Nennett, C.L., 2001. Twenty-four hour activity budgets and patterns of behavior in captive ocelots (Leopardus pardalis). Appl. Anim. Behav. Sci. 71, 67–79.

Wierucka, K., Siemianowska, S., Woźniak, M., Jasnosz, K., Kieliszczyk, M., Kozak, P., Sergiel, A., 2015. Activity budgets of captive Cape fur seals (Arctocephalus pusillus) under a training regime. J. Appl. Anim. Welf. Sci. 19 (1), 62–72. https://doi.org/10.1080/10888705.2015.1106945.