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Risk factors for stereotypic behaviour in captive ungulates

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Behavioural needs are highly motivated actions critical to a species survival and reproduction. Prolonged restriction of these behaviours can lead to stereotypic behaviours (SB) in captive animals, and this is particularly common in ungulate species. While risk factors for SB have been suggested for some ungulates, no study has integrated these findings to identify which aspects of ungulates' wild behavioural biology and captive husbandry are potential drivers for SB across this clade. We collated SB data from 15 236 individuals across 38 ungulate species from 95 sources, and determined species wild/free-ranging behaviour from 559 additional studies. Bayesian-phylogenetic statistical methods showed that ungulate behavioural needs relating to foraging and mating are particularly affected by captive environments, with promiscuous and browsing species showing the greatest prevalence of SB. Concentrate-only diets and lack of *ad libitum* feed substrates were also associated with high SB prevalence. This study identifies which ungulates are better suited to captive environments and which species require targeted husbandry, enrichment and breeding protocols in order to meet their behavioural needs. Our approach of applying Bayesian-phylogenetic inference to factors influencing SB within a clade can be used to identify other intrinsic and extrinsic risk factors of reduced animal health and welfare.

1. Background

Stereotypic behaviours (SBs) are repetitive behaviours induced by frustration, repeated attempts to cope, or central nervous system dysfunction and are widely reported across a variety of captive species [1–4]. From an animal welfare perspective, SB may be indicative of current and/or historic exposure to chronic stress and reduced welfare [3]. These behaviours may also impact animals and their keepers in other ways, for example by reducing the productivity and value of farmed animals [5], reducing performance in sport and companion animal species [6,7], reducing reproductivity in captive animal species [8] and causing clinical injury or trauma to the performing animal or conspecifics (e.g. tail biting in commercial pigs (*Sus scrofa*), feather damaging behaviour in commercial poultry [9] or pet parrots [10]). It is critically important, therefore, that we understand the underlying causal factors of these behaviours. The consequences of not reducing or preventing SB in domestic and captive environments can be significant from production, performance and (most importantly) welfare perspectives.

Behavioural needs are highly motivated behaviours essential to a species survival and reproduction in their ancestral and current wild-ranging environments. Restricting the performance of these behaviours for extended periods thus compromises animal welfare [11]. The majority of animal SB appears to result from the inability to realise these behavioural needs and, over time, the persistent frustration may lead to changes in the central nervous system [1–4]. Although several factors relating to the wild behavioural biology and behavioural needs of single species have already been proposed as key drivers of SB, only a handful of studies have examined the development of SB across a whole taxon. A seminal, systematic analysis of the natural behavioural biology and SB performance of zoo-housed carnivores revealed that home range size and daily travel distances in the wild were the most significant predictors of SB in captivity [12,13]. This challenged the common assumption that the frustration of hunting-based foraging behaviour was the key predictor of reduced welfare in these species. These landmark findings suggested that assumptions regarding SB in other taxonomic groups may be inaccurate, and may ultimately impact the welfare of animals in captivity via unsuitable enclosure designs and inappropriate environmental enrichment protocols. This approach has reframed SB research and has inspired cross-species phylogenetic comparative analyses of captive welfare and/or SB in primates [14], carnivores [15], ruminants [16], parrots [17] and lemurs [18]. These comprehensive, cross-species approaches to understanding SB are of critical importance, particularly for taxa in which these behaviours are prevalent and/or understudied.

Over five billion ungulates are kept as livestock [19] and large numbers are also kept in zoos and safari parks (although the number of individuals in these collections is unknown). This makes ungulates one of the most commonly domesticated taxa. Ungulate species display a range of SB, with oral forms being most common [1]. Examples include oral SBs such as tongue rolling, bar biting and sham chewing in pigs [5], and oral and locomotor SBs such as crib-biting, weaving and box-walking in horses (*Equus caballus*) [20]. Data for exotic ungulate species are sparse [21], with large inter-species differences in the type, prevalence and frequency of SB. For example, it is estimated that 80% of giraffes (*Giraffa camelopardalis*) and okapi (*Okapia johnstoni*) in captivity exhibit at least one form of SB [22], yet in a survey of 25 collections housing banteng (*Bos javanicus*), only two reported any historic occurrence of SB [23]. Although the potential within-species risk factors for SB performance have been identified for some of the most susceptible ungulates, such as giraffe [22], horses [24,25] and pigs [26], this information remains unstudied for the majority of ungulate species.

This study applies a cross-species theoretical framework and novel statistical approach to study SB in ungulates, in which both the species' wild behavioural biology and the study-level captive husbandry risk factors can be explored. Based on the current literature, we derived three primary hypotheses about risk factors for SB development in ungulates, in order to create a framework for the exploratory analysis: (1) ungulates, who display more oral and fewer locomotor forms of SB, would have distinct ecological drivers for SB relating to foraging, eating and processing feed and/or would be kept in environments where these activities are significantly restricted; (2) the disparity between a species natural social organization and their captive conditions may predict SB; (3) ranging and activity patterns would predict SB (see electronic supplementary material for further information about how these hypotheses were derived). We tested these hypotheses by systematically reviewing studies of SB prevalence and type for all ungulate species, alongside information on their behavioural biology relating to (1) feeding and foraging, (2) social organization and mating, and (3) ranging and activity. Using a Bayesian statistical method, that controlled for phylogenetic relatedness, we assessed these potential drivers for the occurrence of SB. Previous cross-species comparisons of captive animal welfare have used species' averages of welfare measures (such as SB or life expectancy), and have therefore not been able to assess the effects of husbandry factors. The innovative statistical approach we apply here, which fits multi-level models in a Bayesian framework, allows the integration of each individual SB study into analyses independently, while controlling for phylogenetic relatedness.

2. Methods

Following seminal work with carnivores [15,16], we developed a novel methodological approach for ungulates that explored potential risk factors derived from a species wild behavioural biology (adjusted to reflect ungulate biology) as well as the current captive husbandry of the subjects within each study.

(a) Stereotypic behaviour and captive husbandry data

Owing to the relative paucity of SB research in exotic ungulates, both SB prevalence and the proportion of time species spent performing SB were initially sourced as output variables, to enable a greater number of species to be included in analyses. SB data from peer-reviewed journal articles and conference abstracts were systematically collated, using the search engines EBSCO Discovery Service and Google Scholar between October 2019 and March 2020. These generated a large number of outputs; thus time constraints prevented the use of additional search engines. Search phrases included all terrestrial ungulate genera, plus terms related to stereotypic, repetitive, and abnormal behaviours (see electronic supplementary material for full search phrase list). Unpublished reports, such as student theses, were also included when encountered. The annual conference proceedings of BIAZA (1999–2017) and AZA (2017–2019) were examined, and authors were contacted where studies were deemed of interest but insufficient information was available. All BIAZA accredited institutions that house ungulates, and had an email or contact form available on their website, were contacted for unpublished data. Sources published before 1990 were excluded, as full versions of these articles were rarely available online. Data from domesticated species were included, as these animals constitute the majority of captive ungulates worldwide.

For inclusion, studies had to involve behavioural data collection over a minimum 24 h window. Ideally, this would have been set as a longer time period; however, in practice, this would have excluded a significant number of studies. Studies were excluded if definitions of SB were not provided, if definitions given were unclear, if definitions were at variance with the standard definition given in the introduction, or where the research was deemed of generally poor quality. Where an ethogram was provided, this was searched to identify behaviours or behavioural groups that fit the definition of SB, and data from these were included. Data from juveniles were not used. To remove transient novelty effects, data from animals experiencing changes to diet, feeding, housing, husbandry, group structure or where new enrichment protocols had been introduced were not used. Where available, baseline data for such studies, prior to the described modifications, were included. Sexes were pooled to increase sample sizes. In addition, although the sex ratios of populations were usually given, it was rarely possible to identify which individuals were stereotypic. Variables recorded were; (1) prevalence of SB within the study population (%), (2) type of SB performed (oral or locomotor; there were some instances of SB that did not fall into these two categories, however, they were only identified in studies that did not meet inclusion criteria),

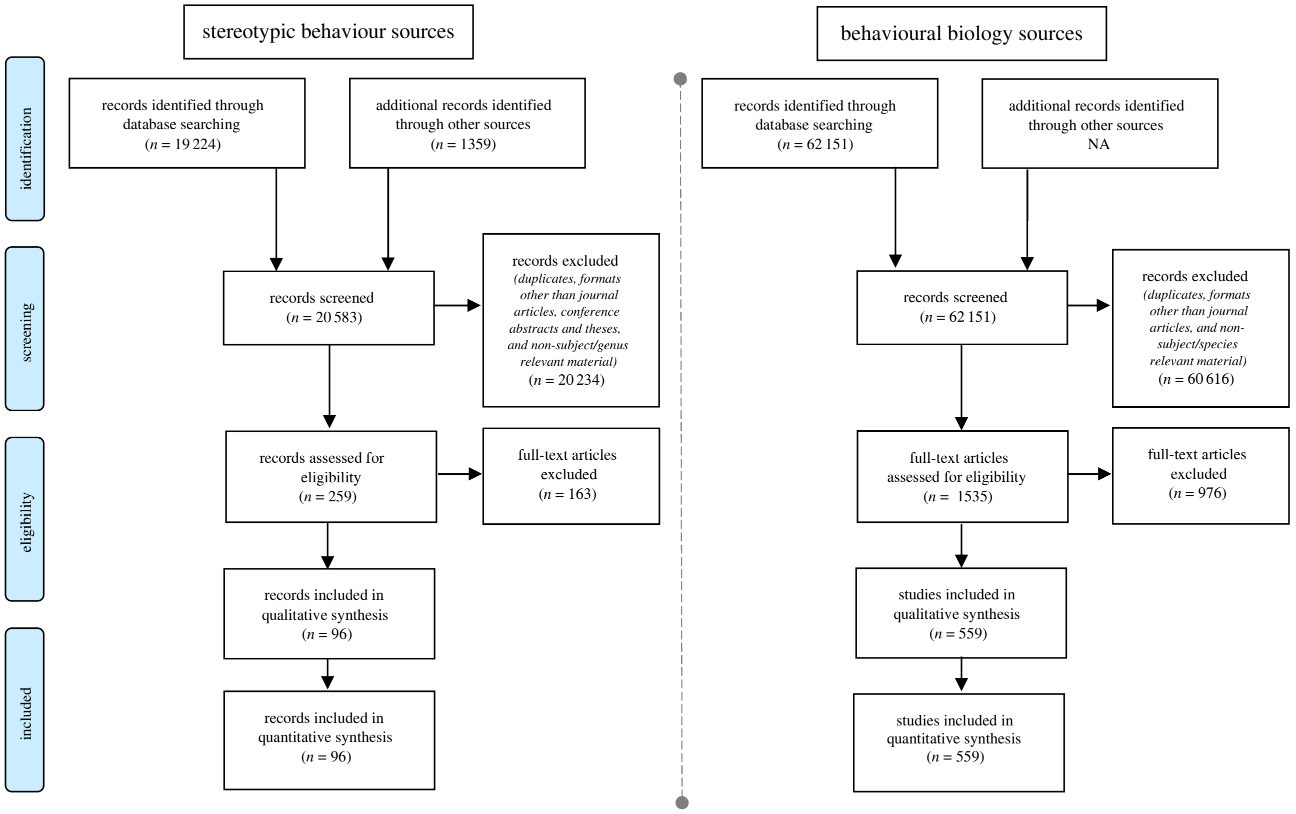

Figure 1. Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) flow diagram [27], showing the number of studies screened and included in analyses for stereotypic behaviour (left) and wild behavioural biology (right) searches. (Online version in colour.)

and (3) the mean proportion of activity budget (%) devoted to performing SB by stereotyping individuals. Where studies only examined one type of SB, oral or motor, this was recorded separately from those which looked at all SB combined. Studies that contained no such data were excluded. A Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) flow diagram of source selection through each phase can be seen in figure 1. A full list of the included studies and extracted raw data are available at https://osf.io/mkcw8/.

For each study that met all inclusion criteria and contained SB data of the required type, the following information, if available, was also recorded:

— Where animals were housed and the year of study. This reduced the risk of non-independent data. In cases where the same species were observed at the same establishment on more than one occasion, both datasets were only included if they were collected greater than 1 year apart. If observations were separated by less than 1 year, means were derived for each variable.
— Area (m^2) of daytime enclosure. Where dimensions were not provided for horse stables or cow tie-stalls, we used dimensions reported in the academic literature for that species, in that country, and less than one year either side of publication. Where this was not available, enclosure area was recorded as NA.
— Sex of observed individuals. Used to calculate the proportion of females in the group.
— Size of daytime social group of observed animals (adults only). Animals were considered as part of the same social group if tactile contact was possible between them.
— Sex composition of daytime social group (adults only).
— Proportion of castrated animals.
— Feed availability. Categorized as ad libitum (animals had feed available at all times) or in meals (animals fed at discrete times of day, with rations not expected to last until the following meal).
— Predominant feed type. Categorized as forage (plant material, either unprocessed or minimally processed, e.g. grass, hay or silage), concentrates, or both. Feed given as part of enrichment was not included.

(b) Wild behavioural biology data

The wild behavioural biology factors used in the models came under the general divisions of diet and feeding, social structure and ranging and activity. Data on species' wild/free-ranging behavioural biology was systematically collated from peer-reviewed journal articles, using the search engines EBSCO Discovery Service and Google Scholar between April and November 2020. For search protocols and inclusion criteria see electronic supplementary material. A PRISMA flow diagram of source selection through each phase can be seen in figure 1. A full list of the included studies and extracted raw data are available at https://osf.io/mkcw8/. For articles remaining after screening, the following information was recorded for the species:

1) Foraging strategy (grazer, browser, mixed feeder, frugivore or omnivore);
2) Time spent eating (% day);
3) Diet diversity (number of different plant genera consumed);
4) Information pertaining to social group size and composition. *Where this differed between the sexes, these were recorded separately;*
5) Mating system type (promiscuity, polygamy or polygyny). *No other mating strategies were observed in the sample;*
6) Time spent active (% day);
7) Home range size (km^2);
8) Distance travelled daily (km);

9) Migration strategy (migratory, non-migratory or mixed strategies within-study population).

Sexes were pooled in all cases, due to a paucity of sex-segregated data. For continuous variables, median values across studies were calculated to give overall species' estimates. For categorical variables, the modal response was determined. Species' average masses were obtained from the PanTHERIA database [28].

(c) Captive/wild comparisons

Two additional variables were derived from the information collected. 'Space availability' (range 0.0–1.0) was calculated as the animal's enclosure size as a proportion of its home range size. 'Group same as wild' was considered 'yes' (Y) if the social conditions in captivity had been observed in any of our wild studies, taking into consideration both the number of animals in a group and the ratio of males:females. 'No' (N) was recorded if the animals were housed in social groups not observed in any of the wild studies identified. We considered using average group size as a predictor however, for many ungulate species, males and females live in groups of very different sizes. An average value would therefore not be representative of either situation. In addition, even where males and females live together, the ratio of the two sexes in a group is rarely even. Unless the sex ratio of a captive group reflects something similar to that experienced in the wild, we expect that this would be stressful to the animal. This variable was derived to avoid these complications. We did not derive any further variables, so as to minimize subjectivity in the dataset.

(d) Statistical analysis

Data were analysed in RStudio v. 1.3.1073 [29]. Multilevel models were fitted within a Bayesian framework as this allowed for both phylogenetic relatedness and repeated measurements within species to be included as random factors in analyses. Bayesian regressions return distribution of possible effect sizes rather than point estimates (as is the case in frequentist regression), with the credible interval (CrI) being the range of this distribution containing a particular percentage of probable values. In this case, we use a 95% CrI. Where a CrI does not contain zero, this suggests an effect is evident. Bayesian regressions, therefore, have the advantage of showing uncertainty in situations where data are limited, as is the case for many species in this study. In addition, estimates can be improved as more data are gathered, allowing for future improvements to regression models.

Pearson correlation coefficients between pairs of all continuous predictor variables, and Cramer's V coefficients between pairs of all categorical predictor variables, were calculated. Where these exceeded 0.90, only one of the variables was included in the models to avoid multicollinearity [30]. As a result, space availability was removed from analyses due to a strong positive correlation ($R^2 = 0.94$) with home range size. Given the significance of home range size found in other species, its inclusion was of higher importance than that of our derived variable. Visual examination of box plots generated from all possible pairs of continuous and categorical variables did not reveal any associations. Body mass, a potential confounding factor, correlated with diet diversity ($R^2 = 0.96$) and proportion of time spent active ($R^2 = 0.91$). Mass was therefore controlled for in models containing these two variables. An exploratory model containing only body mass and our random effects found that mass did not statistically influence SB prevalence (95% CrI [−0.01, 0.02]). Unfortunately, it was not possible, with the data available, to analyse prevalence of locomotor and oral SB separately, so these were combined for SB prevalence models. Similarly, due to lack of available data, the influence of predictor variables on the time spent performing locomotor SB could not be assessed. There were sufficient data, however, to allow for exploratory modelling of the time spent performing oral SB.

The brm function in the brms package [31,32] in RStudio was used to individually test the effect of each predictor variable on SB prevalence and the time spent performing oral SB, using Bayesian regression models (BRMs). Sample size and the volume of missing data precluded the building of multi-factor models, or the inclusion of interaction effects. SB variables were weighted by (log) sample size. Log transformation was used to prevent a handful of particularly large studies having too great an influence over outcomes. Individual study and phylogenetic relatedness were included as random effects. Phylogenetic relatedness was incorporated into models as a covariance matrix. To derive this, 1000 phylogenetic trees for the selected ungulate species were generated from vertlife.org [33], and an average tree calculated using phytools v. 0.7–70 [34]. A covariance matrix was produced from the average tree using ape v. 5.5 [35]. Phylogenetic information was available for all but one species (*Taurotragus oryx*), which subsequently had to be excluded from analyses. It was not possible to include the location of stereotypic animals as a random factor, as it would have reduced the sample size significantly ($n = 62$).

BRMs were fitted with a Gaussian distribution, default priors, a maximum tree depth of 20, and an adapt delta of 0.99 (see *SI appendix*, supplementary text for more information on model fitting and diagnostics). Each BRM was run for two chains of 8000 iterations, discarding the first 1000 as warmup. Statistical inference was determined by examining whether the 95% CrI of the population-level effect (i.e. of predictor variable for the given model) overlapped with zero or not. If less than 10% of the total difference between upper and lower CrI was above or below zero, the association was classified as a trend. For categorical variables, *post-hoc* hypothesis testing using the brms package identified important differences between pairs of groups not included in the model output summary. CrIs for pair-wise comparisons are of the distribution of the difference of the means of the two groups, and statistical inference was determined in the same way as population-level effects, described above. SB prevalence models were run with ($n = 95$) and without ($n = 86$) studies of intensively reared livestock, to check if these skewed findings. Livestock was defined as intensively reared if they were housed in pens or stalls within a barn, with no outdoor access. Conditional effects plots were generated in brms and visualized with ggplot2 [36]. These display model-predicted coefficients with 95% CrIs.

3. Results

Our final dataset of 96 captive animal studies represented 15 263 individuals across 38 species (figure 2). Owing to missing data, no models contained all 96 studies and 38 species. The full list of effect estimates with 95% CrI of risk factors for SB prevalence and proportion of time spent performing oral SB, using categorical and continuous predictor variables, are presented in electronic supplementary material, tables S1–S4. This includes the number of studies included in each model and in each group for categorical variables.

(a) Stereotypic behaviour prevalence

Of the wild behavioural biology variables associated with diet and feeding, feeding strategy was found to be predictive of SB prevalence, with browsers and mixed feeders both

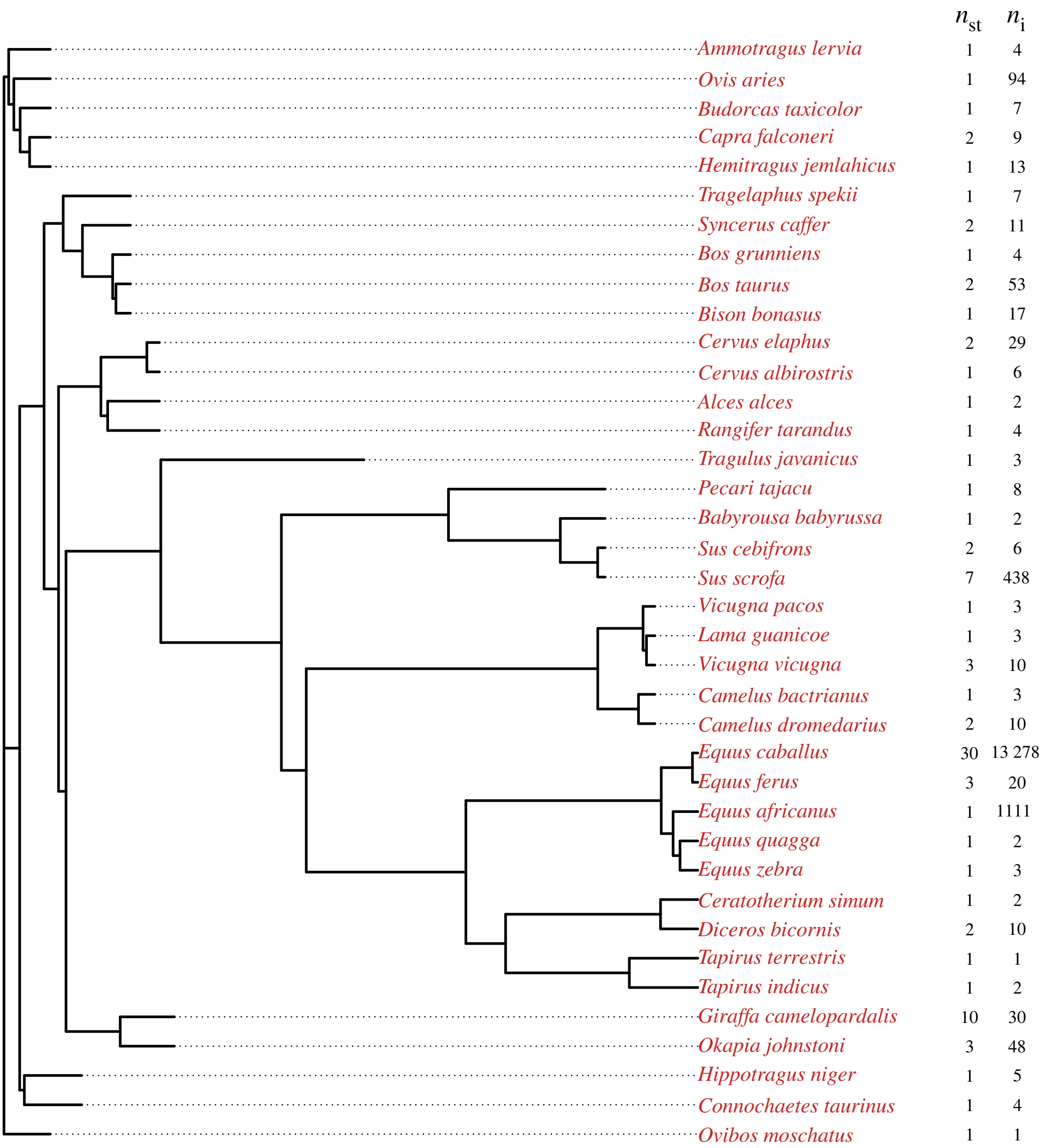

Figure 2. Phylogenetic tree of ungulate species ($n_{sp} = 38$), with the number of stereotypy sources (n_{st}) and the number of individuals (n_i) used in analyses. (Online version in colour.)

exhibiting a higher prevalence than grazers (figure 3; electronic supplementary material, table S1). There was a trend toward omnivores having a greater SB prevalence than grazers, but this appears to have been driven by intensively reared livestock because this trend disappeared following their exclusion from the model (electronic supplementary material, table S1). With intensively reared livestock removed from analyses, in addition to the differences identified in the full model, browsers were found to have a greater prevalence of SB than mixed strategy feeders and omnivores. The proportion of time spent eating and diet diversity did not predict SB (electronic supplementary material, table S2). Of the variables related to husbandry, SB prevalence was higher in animals fed in discrete meals as opposed to *ad libitum*, and in those fed concentrates rather than a forage or a mixed concentrate plus forage diet (figure 3; electronic supplementary material, table S1). Even without the influence of intensively reared livestock, trends toward greater SB in those fed meals, and those fed entirely concentrates rather than forage, were still evident (electronic supplementary material, table S1).

Of the social factors explored, wild mating strategy was found to influence SB (figure 3; electronic supplementary material, table S1). Promiscuous species had a greater prevalence of SB than polygynous ungulates, and this difference remained when intensively reared livestock were removed from the model (electronic supplementary material, table S1). Whether social groups in captivity were similar to those the species experienced in the wild, the proportion of castrated animals in a group, and the proportion of females, did not play a role (electronic supplementary material, tables S1 and S2). When intensively reared livestock were removed from the model, a positive correlation between the proportion of animals castrated and SB prevalence became evident, as did a trend toward a negative correlation between the proportion of females in a group and SB prevalence

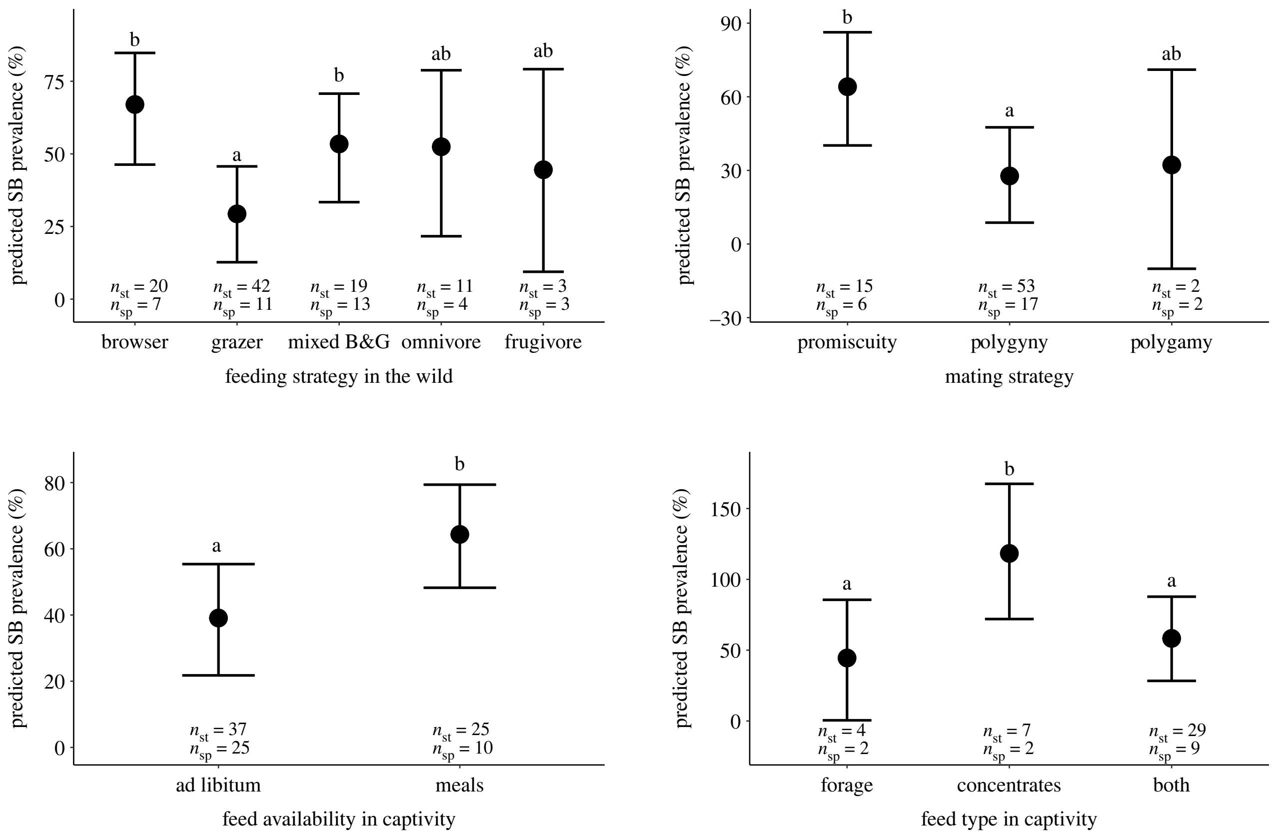

Figure 3. Predicted prevalence of stereotypic behaviour (SB) in captive ungulates by influential wild behavioural biology (top row) and captive husbandry (bottom row) variables. Model-estimated coefficients are shown with 95% CrIs, and sample sizes in terms of number of studies (n_{st}) and number of species (n_{sp}). Coefficients that do not share a letter are different. As plots are of predictive values, some estimates and CrIs fall below zero or above 100%; it should be noted that, in reality, stereotypy prevalence cannot fall below 0% or above 100%. See electronic supplementary material, tables S1 and S2 for coefficient estimates and Bayes factors. When models were re-run without the inclusion of intensively reared livestock, (1) the difference between grazers and mixed feeders weakened to a trend, (2) the difference between browsers and grazers remained, (3) browsers were found to have a greater prevalence of SB than mixed strategy feeders and omnivores, (4) the difference between those fed meals and those fed ab libitum weakened to a trend, (5) the difference between animals fed concentrates and animals fed both concentrates and forage was no longer evident, (6) the difference between concentrates and forage diets weakened to a trend, and (7) there was no change in the effect of mating strategy on stereotypy prevalence.

(electronic supplementary material, table S2). Regarding ranging and movement, enclosure size, proportion of the day spent active in the wild, home range size, migratory strategy and daily travel distance did not influence SB (electronic supplementary material, tables S1 and S2).

(b) Proportion of time spent performing oral stereotypic behaviour

Owing to the paucity of reporting in the majority of studies, analyses on *time spent performing oral SB* were undertaken on small samples, and the number of species included in a given model ranged from three to seven. For categorical variables, some of the groups present in SB prevalence models were not represented, and some groups were represented by just one data point (see electronic supplementary material, table S3, SI Appendix for more information regarding data distribution for these models). We also did not run analyses without intensively reared livestock, as the resulting species sample size would have been too small ($n = 4$) for meaningful interpretation. Results here should therefore be considered exploratory.

Of the wild behavioural biology variables associated with diet and feeding, feeding strategy was predictive of time spent performing oral SB, with omnivores performing more SB than browsers, grazers and mixed strategy feeders (electronic supplementary material, table S3). There was also a strong trend toward a positive correlation between diet diversity and time spent performing oral SB (electronic supplementary material, table S4). Of the variables related to captive husbandry, oral SB performance was greater in animals fed concentrates compared to a forage or a mixed concentrate plus forage diet (electronic supplementary material, table S3). Proportion of time spent eating in the wild, captive feed availability, and all variables associated with sociality and ranging and movement were not predictive of oral SB (electronic supplementary material, tables S3 and S4).

4. Discussion

This work applied a novel statistical approach to study SB in ungulates. Cross-species comparisons of captive animal welfare have, until now, used species' averages of welfare measures (such as SB or life expectancy), and have therefore not been able to control for or assess the effects of husbandry factors. By fitting multi-level models in a Bayesian framework, however, we were able to integrate each individual SB study into analyses independently. This innovative approach allowed for husbandry factors to be accounted for when examining species-level risk factors and data on individual animals to be included in the analyses. This approach offers the potential for understanding the intrinsic species-level risk factors for reduced welfare to an extent not previously possible.

Our data suggest that features of both a species wild behavioural biology and captive husbandry are predictive of SB prevalence in ungulates, with factors falling across two of the three areas we examined: diet and feeding, and social factors. Important predictors of SB prevalence within diet and feeding were feeding strategy in the wild and feed type and availability in captivity. The important social factor was mating strategy in the wild, with the proportion of castrated animals and the proportion of females in a group also predicting SB in models without the presence of intensively reared livestock. None of our ranging and movement factors were predictive of SB. Previous comparable work with carnivores found that factors exclusively relating to ranging (home range size and daily travel distance) were the key predictors of SB, with factors relating to natural foraging being non-significant [12,13]. This highlights the importance of assessing SB risk factors within each clade. In carnivores, as well as in primates [14], pacing SB was predicted by ranging behaviour. Pacing is rare in ungulates, with oral SB being more common, confirming that locomotor and oral SB are likely to have different causal mechanisms. Indeed, our exploratory analyses suggest that feeding factors specifically are predictive of time spent performing oral SB.

Taking each SB driver in turn, within the area of diet and feeding there was a higher prevalence of SB in browsing species and mixed feeders than in grazers. Both differences remained when studies of intensively reared livestock were removed from the model, indicating the effect was not being biased by their presence. Browsing ungulates have highly specialized feeding behaviours to crop forage and negotiate thorns and spines selectively [37]. In addition, during foraging, browsers spend less time ingesting feed than grazers and are required to locate and move between patches, due to the differences in food dispersion [38]. Ethological theories suggest that animals are highly motivated to perform behaviour patterns such as these, and may become frustrated and develop SB when attempts to execute them are thwarted [1]. Replicating the behavioural needs of browsers in captivity, however, is challenging [39,40]. Fresh browse is often replaced with hay and concentrated grain [22], and mimicking the patch distribution of food sources within the confines of an enclosure is difficult. Browsers may therefore use SB as a behavioural alternative where they are unable to fulfil the behavioural motivation to search for and/or consume woody plants. A further feature of browse as a feed source is that it typically occurs in clusters, with ingestion of one cluster potentially stimulating further local food-search behaviour via positive feedback [40]. This will further enhance the behavioural need to browse, which if thwarted may increase the likelihood of SB. Foraging also has functions beyond nutrient intake, playing an important role in maintaining optimal oral and gastrointestinal health [41]. Browsing species, who arguably have the most specialized oral physiology, and face the greatest restrictions on their ingestive and digestive behaviours, are most at risk of reduced health and welfare. Indeed, ruminant species with a natural diet high in browse have a reduced life expectancy (another marker of reduced welfare) in captivity [16], highlighting the importance of meeting the dietary and behavioural feeding needs of browsing animals to improve wellbeing. Providing captive browsing animals with a diet high in fresh browse, alongside the use of enrichment that encourages natural browsing behaviour, is therefore essential for maintaining high welfare. However, it is not completely clear the extent to which adding fresh browse is beneficial to welfare for all ungulates, as in some cases providing additional fresh browse substrate has been shown to increase SB [42]. By contrast, meeting the dietary and ingestive behavioural needs of grazing species is much simpler as grass species are readily available and easy to maintain, and hay provides a more similar replacement when fresh grass is not available, which may explain the lower rates of SB in these species.

Feed type and availability were also predictive of SB, with higher SB rates in those fed concentrates, and in those fed in discrete meals as opposed to *ad libitum*. The differences were still evident, but became less distinct, when intensively reared livestock were removed from models. This provides a good indication that these studies were not solely responsible for the differences seen, however, it is worth noting that only one study of animals fed entirely concentrates remained once livestock was excluded. Meal feeding is often associated with high concentrate diets, however, no strong association between feed type and feed availability was identified prior to modelling. Our data highlight that forage is regularly supplied at discrete time points, rather than ad libitum. It is therefore important to consider feed type and feed-availability separately when considering welfare. Both factors have been linked previously to SB in specific ungulate species, including horses [24,25,43], pigs and cattle (*Bos taurus*) [44] and giraffe and okapi [22]. The inter-species approach undertaken here indicates that providing access to *ad libitum* forage reduces the risk of SB across ungulate species. Given that oral SBs are the most prevalent type of SB in ungulates, and that feeding is frequently suggested to be associated with their performance, it was surprising that time spent eating in the wild did not correlate with SB prevalence [1]. Although strategies to increase the amount of time spent foraging, eating or processing feed have successfully reduced SB performance across a wide range of ungulate species—for example, sheep (*Ovis aries*) [45], cattle [46–48] and giraffe [49,50]—such interventions are not always successful [42,51–55]. Given this variability in success, perhaps it is not the increase in time feeding *per se* that confers the beneficial effect, but rather some other aspect of the interventions. It is also important to note that measures of feeding time rarely include the time spent moving between food patches when browsing or the time spent ruminating, and as such may not be the best overall measure of time spent processing food. Exploratory analyses of time spent performing oral SB further suggest that feeding strategy in the wild and feed type in captivity are specifically predictive of oral SB. Although sample sizes for these models were small ($11 \leq n \geq 21$), representing between three and seven species, these results provide an initial indication that feeding factors may play a role in oral SB development in ungulates; however, more data are needed before conclusions can be drawn.

In terms of social factors, promiscuous species had a higher prevalence of SB than polygynous species, with this effect remaining when intensively reared livestock was removed from the model. In captivity, mating and breeding are regularly controlled, with partners almost always selected based on human management, and in many instances animals of different sexes may never actually meet, yet the effects of these manipulations on welfare are rarely explored. Offering animals choice and control over their environment is considered integral in optimizing their welfare [56]. This may be overlooked in the context of mating and could be an important factor leading to the exhibition SB in captive ungulates. It follows that promiscuous species, who choose new partners most frequently, experience the greatest degree of restriction in captivity, relative to behavioural needs, and are therefore more likely to develop SB as a result. In captive ruminants, monogamous males demonstrate a greater life expectancy than polygamous males [16], further indicating that having an increased number of partners in the wild is a risk factor for reduced welfare in captivity. Allowing mate-choice in captive breeding programmes has already been proposed as a method for improving reproductive success [57,58], and our data suggest that it may also reduce the likelihood of SB, thus improving welfare. Indeed, highly stereotypic mink are less successful in mate choice tests [59], indicating that perhaps promiscuous ungulates are caught in a positive feedback loop, whereby they perform SB due to behavioural mating frustration, but by doing so reduce their reproductive success. Identifying mating system as a predictive factor for SB also highlights the importance of internal cues in eliciting a stereotypic response. Although a large proportion of SBs appears to be anticipatory (i.e. elicited by cues denoting imminent food or access to conspecifics), many SBs occur spontaneously, independent of these events, suggesting that their manifestation reflects a change in the animal's internal state [41]. These putative interoceptive cues are elusive, but are often attributed to the motivation and restricted performance of other species-specific behavioural needs [41]. The data here suggest that reproductive drives are a strong candidate for the motivational origin of cue-independent SB in ungulates. That mating system was not predictive of time spent performing oral SB in our exploratory analyses suggests that, in ungulates, it may be locomotory forms of SB that are cue-independent, although more data are needed to confirm if this is the case.

By contrast to our mating system results, deviations from species' wild social organization when in captivity did not influence SB, despite group size being a risk factor for SB in primates [14], and previous work in ungulates suggesting social factors have been linked to the risk of SB development. For example, in giraffe and okapi, who are naturally solitary or live in small unstable groups, access to conspecifics at night increases stereotypic licking [22] whereas contact with conspecifics reduces the risk of performing SB in horses (which form long-term social bonds) [60]. In our study, the definition of two captive animals being part of the same social group was if tactile interaction was possible between them. Previous work in individually housed ungulates, however, has demonstrated that visual access to conspecifics can also significantly reduce performance of SB in social species [60,61]. Lack of tactile interactions may therefore not play a large role in SB development if visual access is possible.

Interestingly, the proportion of castrated animals and the proportion of females in a group did not correlate with SB prevalence in full models. However, effects were seen with the exclusion of intensively reared livestock, where there was a positive correlation between castration proportion and SB, and a trend toward a negative correlation between proportion of females and SB. Six of the nine intensive livestock studies removed were populations of 100% females, none of which were castrated, all of which had a high SB prevalence, and therefore had a large influence on model outcomes. Previous studies that have identified a relationship between castration and SB in horses have been contradictory [62–64], and indicate that the extreme husbandry and social isolation experienced by the majority of stallions (non-castrated male horses) may be masking castration effects. Our cross-species analyses suggest that castration increases the risk of developing SB. Castration is a painful and stressful event in the life of a young animal [65]. Other stressful early life events, such as weaning and maternal deprivation, have been associated with SB [66,67]. It follows that castration may have a similar effect, and further multi-species studies of early life effects on SB would be useful. The finding that social groups with a higher proportion of females tended toward having a lower prevalence of SB may not be completely independent of the effect of castration, given that it is usually males that are castrated, and that non-castrated males are often housed in isolating environments. It was not possible to include multiple independent variables in our analyses, however, as we expand our dataset going forward, it should become possible to disentangle the effects of sex and castration.

None of the ranging and movement factors examined influenced SB, despite levels of SB being significantly predicted by home range size in carnivores [12,13], and by daily journey length in primates [14]. Although some ungulates have a large annual home range, home ranges usually overlap [68] and movement usually occurs as a slow drift in location during foraging activity rather than as purposeful travel [69]. As directed travel across their home range is not required by most ungulate species, it follows that ungulates may not have an innate need to locomote long distances, thus large home range sizes are not a driver for SB.

(a) Study limitations and future directions

We acknowledge several limitations for this study, many of which were the inevitable result of the paucity of detail provided in the datasets we interrogated. First, we pooled diverse forms of SB despite evidence from several species suggesting that different forms of SB do not share the same aetiology [14,17,70]. Although we set out to analyse oral and locomotor forms separately, the vast majority of published SB prevalence data do not separate the two forms, meaning resulting sample sizes were insufficient for the generation of robust models, and only preliminary analysis of oral SB data could be performed. Previous cross-species analyses of SB in other clades have identified heterogeneity in the causal mechanisms of different types of SB. In primates, daily travel distance in the wild predicted route tracing, whereas natural group size correlated with fur-plucking SB [14]. The effect of home range size in carnivores was greater for route tracing SBs than for all SB forms combined, suggesting that non-route tracing SBs have different drivers [70]. In captive parrots, diet specifically predicted feather-damaging SBs, yet having a larger brain size was associated with oral SB overall and with whole body SB [17]. It is therefore probable that similar differences in aetiology exist between the types of SB in ungulates. Expansion of the ungulate dataset in the future with more complete records, will hopefully allow the exploration of the causal mechanisms of the diverse forms of SB separately for this clade.

For similar reasons, pooling of sexes was unavoidable with the data available. Males and females differ both physiologically and behaviourally and are thus impacted by captivity in disparate ways [71]. As more data become available, analyses should aim to identify the differences in SB drivers between the two sexes. The statistical methods described in this paper would allow such analyses. A further issue was the volume of missing data across both captive environment and wild behavioural biological predictors. This prevented the generation of models containing multiple predictor variables and interaction effects, which would have allowed us to explore the interface between captive environment and wild behavioural biology factors in the development of SB.

It is also important to note that, for some species, sample sizes were very small and this could be considered to be a limitation of the study. However, the benefit of modelling within a Bayesian, rather than frequentist, framework is that it is capable of handling small sample sizes. In addition, analyses were weighted by sample size to ensure these small studies were not overly influential. Given the dearth of SB data available for the majority of ungulate species, non-inclusion of these small studies would have vastly reduced the number of species in analyses and reduced the generalizability of outcomes.

Finally, future research could also profitably extend the number of predictor variables explored. For some potential risk factors (such as territoriality, time spent engaged in social behaviour and weaning age) there were simply insufficient data available. Physical enrichment is commonly used to prevent or reduce SB and it would have been beneficial to include data on this in analyses although it is arguably impossible to systematically and fairly categorize physical enrichment in ungulates. For grazing species, for example, living in a large grass pasture is highly enriching in itself, but would not be categorized as an enrichment device or as a complex environment. Indeed, enrichment is (relative to carnivores and primates [72]) rarely provided for ungulates, except for those kept in highly confined conditions such as production animals (e.g. pigs kept in the EU [73]) and some zoo animals (e.g. giraffe [74]). With a larger, more complete, sample, multiple-predictor models would potentially circumvent such contradictions. An outline of the desired attributes of a zoo or livestock study, in order to allow more effective inter- and intra-species comparisons in the future, can be found in electronic supplementary material, table S5.

5. Conclusion

There is still much to be understood regarding the drivers of SB in captive ungulates and, with the addition of extra data, future studies using our ungulate model could explore, in depth, the potential differences in the motivational drivers between oral and locomotor SB. Given the contrast between the results of our study and those investigating carnivores and primates, exploring these differences in drivers remains an important avenue for future research.

Using our approach, it is now possible to use captive husbandry and wild behavioural biological predictors of SB to determine the likelihood of an ungulate species developing SB, even when there is a lack of empirical evidence for that species. Our results raise concerns about the suitability of certain ungulate species for captivity and suggest that current captive environments are not able to accommodate the behavioural needs of promiscuous and browsing species. From our dataset, okapi, giraffe, black rhino, camel and domestic pigs are some of the species at highest risk of SB, however it is also important to consider the welfare of browsing and promiscuous species that are understudied and thus not represented in our study. Knowing which species are at high risk, it would be beneficial for collections to focus on species at lower risk of SB in order to promote good welfare, such as southern white rhino, Sable's antelope or common wildebeest. Where browsing species are already housed in captivity, the use of targeted environmental enrichment, which encourages the specialized feeding behaviours of the species and allows for movement between food patches, is essential for improving welfare. Identification of the risk factors associated with captive husbandry also provides practical insight into strategies to reduce SB and improve the welfare of captive ungulates, by providing low concentrate, high forage diets with ad libitum access to feed substrates. For species identified as at high risk, there needs to be a real effort to understand how we can better meet the needs of these species in captivity via targeted husbandry, enclosure design, environmental enrichment and modification of breeding programmes. This study also identified gaps in ungulate SB research that, if carried out, would greatly increase the robustness of the statistical model. In particular, there needs to be greater documentation of the epidemiology of locomotory SB in a range of captive ungulate species.

More broadly, our statistical approach provides a methodology for future cross-species comparisons of markers of poor (or good) welfare, that can incorporate analyses of species-level and study/individual-level risk factors and can be used in a wide range of welfare and conservation contexts.

Data accessibility. The full list of included studies, raw data and R scripts have been deposited in Open Science Framework (OSF) and can be accessed via https://osf.io/mkcw8/.

The data are provided in electronic supplementary material [75].

Authors' contributions. K.L.: conceptualization, formal analysis, investigation, methodology, writing—original draft; M.O.P.: conceptualization, funding acquisition, methodology, supervision, writing—review and editing; L.P.: conceptualization, funding acquisition, methodology, supervision, writing—review and editing; S.D.M.: conceptualization, methodology, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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