

Supplementary Information for:

Risk factors for stereotypic behaviour in captive ungulates

K. Lewis, M.O. Parker, L. Proops, and S.D. McBride

Corresponding authors: Sebastian McBride and Kate Lewis

Email: sdm@aber.ac.uk, kate.lewis@port.ac.uk

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Background

Generation of hypotheses

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. The first hypothesis was that 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. A previous cross-species analysis found that discrepancies between captive and wild diets are negatively correlated with relative life expectancy in ruminants, a sub-group of ungulates (1). Reduced relative life expectancy is considered a proxy for poor welfare, as are high levels of SB. Potentially, therefore, species who face the greatest restrictions to their dietary behavioural needs in captivity are potentially more susceptible to SB and compromised welfare. In free-ranging conditions, ungulates may devote up to one third of their time to eating (2). Feeding behaviour can be markedly altered in domestic and captive environments, either in terms of diet (3) or reduced feeding, ingestion and processing time (4). Thus, the captive environment has the opportunity to produce unsatiated feeding motivation, either behaviourally or nutritionally, and this is considered to be the primary basis for oral SB development in ungulates (5). Although this hypothesis states that oral, and not locomotory, SBs are associated with feeding factors, a number of studies have also reported anticipatory pre-prandial locomotory SB associated with food arrival for some individuals within some ungulate species (6,7). Locomotory SB may therefore also reflect sustained levels of feeding-related motivation and one of the aims of the proposed analysis is to better understand whether different underlying risk factors (captive husbandry and wild behavioural biology) at both the individual and species level exist between the two forms of SB.

The second hypothesis was that the disparity between a species' natural social organisation and their captive conditions may predict SB. Ungulates display a wide range of social, territorial and reproductive behaviours; from being almost entirely solitary, to living in large stable social groups (8). Mating systems range from monogamous pairs, through harems, to highly polygynous leks (9). In captivity, group composition and mating are highly controlled, and castration is common in some species, potentially preventing individuals from meeting their social behavioural needs. In zoo-housed primates, natural social group size was identified as a risk factor for SB (10), and monogamous male ruminants demonstrate a greater relative life expectancy than polygamous males (1), suggesting that social factors could be predictors of ungulate welfare and a species' proclivity to perform SB.

The third hypothesis was centred around potential risk factors relating to ranging and activity patterns. As with feeding and social parameters, there is considerable variation in ungulate species' home range sizes (11), migratory patterns, (12,13), and territoriality (14). Activity levels and time budgets differ significantly between species; mouse deer (*Tragulus kanchil*), for example, spend less than 5% of a 24hr period active, whereas giraffe are active for more than 90% of the day (15,16). In captivity the home range of an individual is artificially restricted, migratory behaviours are prevented, and activity budgets are altered, yet we know very little about how these constraints of behavioural needs affect animals. Levels of SB were significantly predicted by home range size and daily travel distances in carnivores (17,18), and daily journey length and stereotypic pacing were positively correlated in captive primates (10). We therefore hypothesised that these factors may also play a role in SB development in ungulates.

Methods

Stereotypy search protocols

The following search phrases were utilised to search material in EBSCO discovery. Given the size of the ungulate clade, and the standard practice of including the Latin names for study species in scientific research, common names were not used.

- Stereotypy AND *genus* (see below for list of genera used)
- Stereotypic AND *genus*
- “Repetitive behaviour” AND *genus*
- “Repetitive behavior” AND *genus*
- “Abnormal behaviour” AND *genus*
- “Abnormal behavior” AND *genus*

Genera searched:

<i>Equus</i>	<i>Tapirus</i>	<i>Ceratotherium</i>	<i>Dicerorhinus</i>
<i>Diceros</i>	<i>Rhinoceros</i>	<i>Camelus</i>	<i>Lama</i>
<i>Vicugna</i>	<i>Tayassu</i>	<i>Catagonus</i>	<i>Pecari</i>
<i>Sus</i>	<i>Porcula</i>	<i>Hylochoerus</i>	<i>Potamochoerus</i>
<i>Phacochoerus</i>	<i>Babyrousa</i>	<i>Hyemoschus</i>	<i>Moschiola</i>
<i>Tragulus</i>	<i>Antilocapra</i>	<i>Okapia</i>	<i>Giraffa</i>
<i>Alces</i>	<i>Capreolus</i>	<i>Blastocerus</i>	<i>Hippocamelus</i>
<i>Mazama</i>	<i>Odocoileus</i>	<i>Ozotoceros</i>	<i>Pudu</i>
<i>Rangifer</i>	<i>Axis*</i>	<i>Cervus</i>	<i>Dama</i>
<i>Elaphurus</i>	<i>Hyelaphus</i>	<i>Panolia</i>	<i>Rucervus</i>
<i>Rusa</i>	<i>Elaphodus</i>	<i>Muntiacus</i>	<i>Hydropotes</i>
<i>Moschus</i>	<i>Aepyceros</i>	<i>Beatragus</i>	<i>Damaliscus</i>
<i>Alcelaphus</i>	<i>Connochaetes</i>	<i>Ammodorcas</i>	<i>Antidorcas</i>
<i>Antilope</i>	<i>Eudorcas</i>	<i>Gazella</i>	<i>Litocranius</i>
<i>Nanger</i>	<i>Procapra</i>	<i>Pantholops</i>	<i>Saiga</i>
<i>Dorcatragus</i>	<i>Hippopotamus</i>	<i>Madoqua</i>	<i>Neotragus</i>
<i>Oreotragus</i>	<i>Ourebia</i>	<i>Raphicerus</i>	<i>Tetracerus</i>
<i>Boselaphus</i>	<i>Bubalus</i>	<i>Bos</i>	<i>Pseudoryx</i>
<i>Syncerus</i>	<i>Bison</i>	<i>Tragelaphus</i>	<i>Taurotragus</i>
<i>Budorcas</i>	<i>Ovibos</i>	<i>Choeropsis</i>	<i>Ammotragus</i>
<i>Arabitragus</i>	<i>Capra</i>	<i>Hemitragus</i>	<i>Ovis</i>
<i>Nilgiritragus</i>	<i>Pseudois</i>	<i>Capricornis</i>	<i>Nemorhaedus</i>
<i>Oreamnos</i>	<i>Rupicapra</i>	<i>Cephalophinae</i>	<i>Philantomba</i>
<i>Sylvicapra</i>	<i>Hippotragus</i>	<i>Oryx</i>	<i>Addax</i>
<i>Pantholops</i>	<i>Pelea</i>	<i>Kobus</i>	<i>Redunca</i>

* Due to such a high number of returns using a standard search (n = 30,708), an advanced search of abstracts only was performed for this genus.

Behavioural biology search protocols

EBSCO search

The following two search ‘phrases’ were used to search abstracts on EBSCO Discovery, using the advanced search function:

- “species common name” AND “descriptor”
- “species scientific name” AND “descriptor”

The majority of species have a number of common names, which differ by region and country. For each species, the most widely used common name (in English) was used. Scientific names were also included in the search, to reduce the impact of missing out lesser-used and non-western common names.

For some domestic species (shown underlined below) it was necessary to include additional terms to searches, to prevent becoming overwhelmed with captive animal studies. As domestic species do not naturally occur in the wild, we used feral and free-ranging populations as the closest available proxy for how they would behave without human intervention. The modified search 'phrases' for underlined domestic species were:

- "species common name" AND feral AND "descriptor"
- "species common name" AND free-ranging AND "descriptor"
- "species scientific name" AND feral AND "descriptor"
- "species scientific name" AND free-ranging AND "descriptor"

Species identifiers used were as follows:

<i>Species common name</i>	<i>Species scientific name</i>
African buffalo	<i>Syncerus caffer</i>
Alpaca	<i>Vicugna pacos</i>
Babirusa	<i>Babyrousa babyrussa</i>
Bactrian camel	<i>Camelus bactrianus</i>
Barbary sheep	<i>Ammotragus lervia</i>
Black rhino*	<i>Diceros bicornis</i>
Blue wildebeest	<i>Connochaetes taurinus</i>
Brazilian tapir	<i>Tapirus terrestris</i>
<u>Cattle</u>	<i>Bos taurus</i>
Collared peccary	<i>Pecari tajacu</i>
Common Eland	<i>Taurotragus oryx</i>
Domestic yak	<i>Bos grunniens</i>
Dromedary camel	<i>Camelus dromedarius</i>
<u>Donkey</u>	<i>Equus asinus</i>
Dorcas gazelle	<i>Gazella dorcas</i>
European bison	<i>Bison bonasus</i>
Giraffe	<i>Giraffa camelopardalis</i>
Guanaco	<i>Lama guanicoe</i>
Himalayan tahr	<i>Hemitragus jemlahicus</i>
<u>Horse</u>	<i>Equus ferus caballus</i>
Indian rhino*	<i>Rhinoceros unicornis</i>
Java mouse deer	<i>Tragulus javanicus</i>
Malayan tapir	<i>Tapirus indicus</i>
Markhor	<i>Capra falconeri</i>
Moose	<i>Alces alces</i>
Mountain zebra	<i>Equus zebra</i>
Musk ox	<i>Ovibos moschatus</i>
Okapi	<i>Okapia johnstoni</i>
<u>Pig</u>	<i>Sus scrofa</i>
Plains zebra	<i>Equus quagga</i>
Przewalski's horse	<i>Equus ferus przewalski</i>
Red deer	<i>Cervus elaphus</i>
Reindeer	<i>Rangifer tarandus</i>
Sable antelope	<i>Hippotragus niger</i>
<u>Sheep</u>	<i>Ovis aries</i>
Sitatunga	<i>Tragelaphus spekii</i>
Takin	<i>Budorcas taxicolor</i>
Vicuna	<i>Vicugna vicugna</i>

Visayan warty pig	Sus cebifrons
White-lipped deer	Cervus albirostris
White rhino*	Ceratotherium simum

Behavioural ecology descriptors used were:

Descriptor
Diet
Feed*
Activity
Social
Mating
Hierarchy
Range
Distance
Territor*
Travel
Ruminat*
Mass
Weight

All possible combinations of species identifiers and behavioural ecology descriptors were included.

Google Scholar search

The same search protocol was utilised for the Google Scholar search, with some small modifications:

1. Only titles were searched. There is no abstract search function available in Scholar, and broad searches in such a large database return such huge numbers that it would have been logistically impossible to conduct in the context of this study.
2. Use of the asterisk character to include alternative word forms is not possible in Scholar. The list of behavioural ecology descriptors was adjusted to reflect this:

Descriptor
Diet
Feed
Feeding
Activity
Social
Mating
Hierarchy
Range
Distance
Territory
Travel
Ruminate
Rumination
Mass
Weight

- For rhinoceros species searching, the word 'rhino*' was replaced by two separate searches for 'rhino' and 'rhinoceros'.

Wild behavioural biology inclusion and exclusion criteria

Articles were excluded if animals were:

- In captivity*
- Raised in captivity
- Herded
- Corralled overnight
- Provided with supplementary feed
- Partially managed or only semi-free ranging
- They used data collated from other studies or sources, where it was not possible to confirm if this would lead to double counting of subjects

* In the cases of animals kept in large reserves/fenced areas (for protection from poachers or to prevent free-ranging livestock species from encroaching on non-permitted land), articles were excluded if the enclosed area < the maximum of the mean home range sizes recorded across all included studies for that species. Where this was not available, data from the closest taxonomically related species, for which home range data were available, was utilised. If two or more species were equally closely related, the species closest in mass to the selected species was chosen.

Articles were also excluded if:

- Methods were inadequately described
- They did not contain information pertaining to any of parameters described in the inclusion table below

Parameter	Inclusion criteria
Feeding strategy	<ul style="list-style-type: none"> • This was an outcome of this research (i.e. not a comment in the introduction or discussion). • <i>Categorised as browser (B), grazer (G), mixed browser and grazer (M), frugivore (F), or omnivore (O).</i>
Time spent eating (% of day)	<ul style="list-style-type: none"> • This was an outcome of this research. • Behavioural data were collected for a minimum of 24 hours. • This was not calculated using camera trap data.
Diet diversity (number of different plant genera consumed)	<ul style="list-style-type: none"> • This was an outcome of this research. • Plants were identified to at least genera level.
Social group information	<ul style="list-style-type: none"> • This was an outcome of this research or was observed during the study.
Mating system type	<ul style="list-style-type: none"> • This was an outcome of this research or was observed during the study. • <i>Categorised as promiscuous (Prom), polygynous (PGN), or polygamous (PGM). No other strategies were identified in this group of species.</i>

Time spent active (% day)	<ul style="list-style-type: none"> • This was an outcome of this research. • Behavioural data were collected for a minimum of 24 hours. • This was not calculated using camera trap data.
Mean home range size (km ²)	<ul style="list-style-type: none"> • This was an outcome of this research. • Home ranges are annual (i.e. give the area covered by an individual over a period of 11 – 13 months) or multiannual. Seasonal home range data were not included. • Where more than one method was used for defining home range size, data derived using the minimum convex polygon (MCP) were selected. If this was not available KDE estimates were utilised. • Where home ranges were calculated using multiple contour proportions, the data derived using the highest number of contours were used.
Distance travelled daily (km)	<ul style="list-style-type: none"> • This was an outcome of this research. • Locations were logged at a maximum interval of 24 hours.
Migration	<ul style="list-style-type: none"> • Animals had to be observed or tracked migrating during the study. • It was assumed that if animal locations had been identified for a minimum of one year, yet the study did not mention migration, that the population was non-migratory. • <i>Categorised as migratory (M), non-migratory (N), or mixed strategy (MX).</i>

Data from figures were used where it was possible to do this with a reasonable level of accuracy. Attempts were made to source information on territoriality, group hierarchy, time spent ruminating, and time spent engaged in social behaviour, however searches did not generate sufficient data for these variables to be included in analyses.

Four researchers, including the lead researcher, conducted full-text screening and extraction of wild behavioural biology data. All were trained by the lead researcher. As part of the training process, all researchers independently screened the same sub-set of five articles to ensure agreement with the lead researcher. Additional training was given to any researchers who did not agree with the lead researcher, followed by reassessment. The lead researcher also conducted post-hoc checks of all other researcher's outputs.

Bayesian regression models

Bayesian Regression Models (BRMs) fitted with the brm function in the brms package allow for a high level of model specification (1,2). We tested using default (flat) priors as analyses were exploratory, rather than testing directional hypotheses. The arguments 'chains', 'iterations', 'warmup' and 'thinning' control the sampling and inference behaviour of the model. The settings utilised in this case (chains = 2, iterations = 8000, warmup = 1000, thinning = 1) were selected after initial experimentation, and were a trade-off between computation time, processing power requirements, and the quality of model output (see diagnostics below). The behaviour of the sampler can also be controlled using the adapt_delta and max_treedepth arguments. Increasing these values above default improves the validity of posterior draws. Adapt_delta was set to a high value (max = 1) as we initially experienced issues with divergent transitions. We recommend reading the cited texts for more information on fitting BRM models using the brms package (1–3).

Model diagnostics

A number of diagnostic techniques were used for each model, to ensure a high level of model fit throughout. The 'summary' argument provided R_{hat} values for models. R_{hat} is a measure of chain convergence, with a value of 1.0 denoting complete convergence. Caterpillar plots of the two chains were also created using the 'plot' argument, to provide a further check of chain convergence. In all models, we used $R_{hat} < 1.02$ and oscillating caterpillar plots to indicate chain convergence. Where $R_{hat} > 1.02$, the number of iterations was increased by 2000 and the model re-run. This continued until $R_{hat} < 1.02$.

Posterior prediction plots were then generated using the 'pp_check' argument. Models were accepted if posterior predictions largely picked up on the bimodality and pattern of the observed y -values. When running our initial models, a variety of distributions were tested to see which produced the best fitting posterior plots. Only a gaussian-fitted model was capable of picking up on the bimodality of y values at all, which is why this distribution was selected.

Finally, posterior checks of collinearity were undertaken using the 'pairs' argument. Plots were visually examined for collinearity in predictor variables (both fixed and random effects). Although there were some weak associations noted between intercepts and predictor variables in a handful of cases, no strong relationships between pairs of predictor variables were observed in any model.

Supplementary tables

Table S1. Risk factors for stereotypic behaviour prevalence in captive ungulates, from brm Bayesian multilevel models, using categorical predictor variables.

Hypothesis category	Variable	Stereotypy prevalence							
		Full model (n _{studies} = 95)				Intensively reared livestock removed (n _{studies} = 86)			
		n	Hypothesis	Effect Estimate [95% CrIs]	Baye's factor	n _{groups}	Hypothesis	Effect Estimate [95% CrIs]	Baye's Factor
Diet and feeding	Feeding strategy	n _{studies} = 95 n _{species} = 38	Fr > B G > B	-22.03 [-58.94, 15.49] -37.27 [-56.95, -15.88]	5.31 x 10 ⁸	n _{studies} = 86 n _{species} = 36	Fr > B G > B	-38.15 [-80.52, 5.22] -40.30 [-62.22, -15.88]	4.98 x 10 ⁸
		B=20 BG=19 Fr=3 G=42 O=11	BG > B O > B Fr > G Fr > BG Fr > O G > O G > BG O > BG	-13.55 [-31.38, 4.29] -14.66 [-45.44, 15.73] 15.2 [-14.22, 45.00] -8.48 [-38.37, 22.46] -7.37 [-36.58, 22.43] -22.58 [-45.79, 2.13] -23.69 [-36.44, -10.27] -1.11 [-25.60, 22.89]		B=20 BG=18 Fr=3 G=41 O=4	O > B Fr > G Fr > BG Fr > O G > O G > BG O > BG	-24.00 [-45.39, -2.55] -43.01 [-81.21, -4.14] 2.15 [-31.63, 36.28] -14.15 [-49.63, 21.74] 4.86 [-30.91, 42.16] 2.71 [-26.76, 33.35] -16.3 [-31.99, 0.29] -19.01 [-49.48, 11.72]	
		Captive feed availability	n _{studies} = 62 n _{species} = 31 M=25 AL=37	M > AL		25.32 [14.29, 37.25]	3.26 x 10 ¹²⁴	n _{studies} = 54 n _{species} = 29 M=18 AL=36	
	Captive feed type	n _{studies} = 40 n _{species} = 15 Bo=29 C=7 F=4	C > Bo F > Bo C > F	60.49 [18.74, 103.55] -14.19 [-51.35, 21.17] 74.67 [27.02, 123.00]	1.54 x 10 ¹⁴⁸	n _{studies} = 32 n _{species} = 12 Bo=28 C=1 F=3	C > Bo F > Bo C > F	41.12 [-57.11, 140.77] -37.98 [-96.35, 20.35] 79.10 [-14.99, 174.38]	1.03 x 10 ¹⁴⁶
Social	Mating strategy	n _{studies} = 70 n _{species} = 25 P=15 PM=2 PN=53	PN > PM P > PM P > PN	-4.12 [-8.55, 74.66] 31.94 [-8.55, 74.66] 36.06 [14.72, 56.65]	2.00 x 10 ⁴⁶	n _{studies} = 62 n _{species} = 23 P=7 PM=2 PN=53	PN > PM P > PM P > PN	-0.15 [-41.71, 40.89] 23.29 [-19.59, 66.33] 23.44 [0.65, 46.16]	6.53 x 10 ⁴¹
	Comparable social group	n _{studies} = 70 n _{species} = 31 N=26 Y=44	Y > N	6.55 [-3.38, 16.25]	6.21 x 10 ¹⁰²	n _{studies} = 62 n _{species} = 30 N=24 Y=38	Y > N	12.06 [-2.17, 25.68]	3.28 x 10 ⁹⁸
Ranging and movement	Migratory strategy	n _{studies} = 75 n _{species} = 24 NM=62 Mi=4	NM > Mi Mx > Mi Mx > NM	7.46 [-22.49, 38.25] 2.85 [-38.34, 45.32] -4.61 [-30.27, 22.15]	9.65 x 10 ³⁷	n _{studies} = 66 n _{species} = 22 NM=53 Mi=4	NM > Mi Mx > Mi Mx > NM	7.71 [-23.14, 38.76] 7.47 [-32.56, 49.18] -0.24 [-25.26, 25.98]	9.28 x 10 ³⁴

		MX=9				MX=9			
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Effect estimates and credible intervals (Cris) for variables where stereotypy prevalence differed between groups are shown in bold. Where a trend towards a difference between groups was found, Cris are shown in italics. Bayes factors compare models with a null model containing only phylogenetic information and study as a random factor. Abbreviations are as follows; Fr = frugivore, B = browser, G = grazer, BG = mixed feeder, O = omnivore, M = meal fed, AL = *ad libitum* fed, C = concentrate diet, F = forage diet, Bo = diet of both concentrates and forage, PN = polygyny, P = promiscuity, PM = polygamy, Y = social group is comparable, N = social group is not comparable, NM = non-migratory, Mi = migratory, Mx = mixed populations of migratory and non-migratory animals.

Table S2. Risk factors for stereotypic behaviour prevalence in captive ungulates, from brm Bayesian multilevel models, using continuous predictor variables.

Hypothesis category	Variable	Stereotypy prevalence					
		Full model			Intensively reared livestock removed		
		n	Effect estimate [95% CrIs]	Baye's factor	n	Effect estimate [95% CrIs]	Baye's factor
Diet and feeding	Time spent eating (% day)	n _{studies} = 57 n _{species} = 16	0.04 [-1.73, 1.66]	1.39 x 10 ⁷⁷	n _{studies} = 56 n _{species} = 15	-0.18 [-2.20, 1.77]	1.36 x 10 ⁵⁰
	Diet diversity*	n _{studies} = 49 n _{species} = 26	0.10 [-0.91, 1.29]	1.23 x 10 ¹⁴⁶	n _{studies} = 40 n _{species} = 24	0.41 [-0.97, 1.87]	4.42 x 10 ¹⁴⁴
Social	Proportion castrated	n _{studies} = 42 n _{species} = 13	-4.32 [-42.14, 33.03]	4.45 x 10 ¹¹⁹	n _{studies} = 34 n _{species} = 11	37.21 [13.11, 60.43]	6.03 x 10 ¹¹⁷
	Proportion females	n _{studies} = 86 n _{species} = 37	8.11 [-9.53, 25.00]	1.60 x 10 ⁴⁵	n _{studies} = 77 n _{species} = 35	<i>-17.63 [-36.03, 1.19]</i>	4.14 x 10 ⁴⁵
Ranging and movement	Home range size (km ²)	n _{studies} = 72 n _{species} = 21	1.43 x 10 ⁻³ [6.81 x 10 ⁻³ , 9.45 x 10 ⁻³]	3.19 x 10 ⁴⁰	n _{studies} = 63 n _{species} = 19	3.61 x 10 ⁻³ [4.63 x 10 ⁻³ , 11.41 x 10 ⁻³]	9.84 x 10 ³⁷
	Time spent active (% day)*	n _{studies} = 21 n _{species} = 10	1.20 [-0.46, 3.46]	5.44 x 10 ²⁰⁵	n _{studies} = 21 n _{species} = 10	0.41 [-0.32, 2.74]	1.82 x 10 ¹⁷⁹
	Daily travel distance (km)	n _{studies} = 64 n _{species} = 16	0.41 [-2.22, 3.37]	1.54 x 10 ⁵³	n _{studies} = 55 n _{species} = 14	0.28 [-2.50, 3.20]	1.24 x 10 ⁵⁰
	Enclosure area (m ²)	n _{studies} = 55 n _{species} = 30	1.56 x 10 ⁻⁶ [2.64 x 10 ⁻⁵ , 2.26 x 10 ⁻⁵]	7.76 x 10 ¹²⁴	n _{studies} = 48 n _{species} = 28	1.22 x 10 ⁻⁵ [7.69 x 10 ⁻⁵ , 4.89 x 10 ⁻⁵]	4.05 x 10 ¹¹³

Effect estimates and credible intervals (CrIs) for variables that correlated with stereotypy prevalence are shown in bold. Where a trend towards a correlation was found, CrIs are shown in italics. Bayes factors compare models with a null model containing only phylogenetic information and study as a random factor. *Models included mass as a confounding variable.

Table S3. Risk factors for time spent performing oral stereotypic behaviour (% day) in captive ungulates, from brm Bayesian multilevel models, using categorical predictor variables.,

Hypothesis category	Variable	Time spent performing oral stereotypy (% day)				Comments on data distribution
		n	Hypothesis	Effect Estimate [95% CrIs]	Baye's factor	
Diet and feeding	Feeding strategy	n _{studies} = 21 n _{species} = 7	G > B BG > B O > B G > O G > BG O > BG	9.12 [-15.52, 36.40] -0.64 [-39.56, 39.70] 37.63 [5.16, 71.74] -28.51 [-55.28, -1.36] 9.76 [-21.85, 42.55] 38.27 [1.01, 74.99]	1.10 x 10⁶	No frugivores in model, and mixed feeding strategies are only represented by one data point (sheep).
	Captive feed availability	n _{studies} = 17 n _{species} = 7	M > AL	8.06 [-14.43, 32.68]	3.84 x 10 ⁷	Giraffe (n=9) and horses (n=5) over-represented in this model, so their home range sizes dominate.
	Captive feed type	n _{studies} = 15 n _{species} = 6	C > Bo F > Bo C > F	62.89 [36.40, 89.45] -1.30 [-28.10, 27.15] 64.19 [35.28, 93.03]	1.27 x 10 ¹⁵	Only one data point for concentrates, and one data point for forage. All others (n=13) were mixed diet.
Social	Mating strategy	n _{studies} = 11 n _{species} = 5	P > PN	11.92 [-34.12, 59.02]	1.45 x 10 ¹³	Only promiscuity and polygyny in model, and all polygynous data points were from the same species (horses)
	Comparable social group	n _{studies} = 20 n _{species} = 6	Y > N	4.80 [-17.80, 26.78]	5.74 x 10 ⁻⁴	
Ranging and movement	Migratory strategy	n _{studies} = 19 n _{species} = 6	NM > Mx	-13.03 [-59.85, 32.75]	2256.30	Only compares non-migrators (n=18) with mixed strategy (n=1)

Effect estimates and credible intervals (CrIs) for variables where stereotypy prevalence differed between groups are shown in bold. Bayes factors compare models with a null model containing only phylogenetic information and study as a random factor. Abbreviations are as follows; B = browser, G = grazer, BG = mixed feeder, O = omnivore, M = meal fed, AL = *ad libitum* fed, C = concentrate diet, F = forage diet, Bo = diet of both concentrates and forage, PN = polygyny, P = promiscuity, Y = social group is comparable, N = social group is not comparable, NM = non-migratory, Mx = mixed populations of migratory and non-migratory animals.

Table S4. Risk factors for time spent performing oral stereotypic behaviour (% day) in captive ungulates, from brm Bayesian multilevel models, using continuous predictor variables.

Hypothesis category	Variable	Time spent performing oral stereotypy (% day)			Comments on data distribution
		n	Effect estimate [95% CrIs]	Baye's factor	
Diet and feeding	Time spent eating (% day)	n _{studies} = 16 n _{species} = 4	-0.22 [-1.56, 0.97]	5.89 x 10 ⁹	Giraffe (n=9) and horses (n=5) over-represented in this model, so their data dominate. Other species present are cattle (n=1) and sheep (n=1).
	Diet diversity	n _{studies} = 19 n _{species} = 6	<i>0.81 [-0.07, 1.72]</i>	234.40	Giraffe (n=9) and horses (n=5) over-represented in this model, so their data dominate.
Social	Proportion castrated	n _{studies} = 13 n _{species} = 6	16.33 [-13.23, 43.65]	<u>1.17 x 10¹¹</u>	Seven of the 13 data for castration in this model are 0.
	Proportion females	n _{studies} = 21 n _{species} = 7	0.65 [-26.13, 26.96]	<u>29.22</u>	Uses all available data
Ranging and movement	Home range size (km ²)	n _{studies} = 19 n _{species} = 6	2.04 x 10⁻³ [8.64 x 10⁻³, 4.40 x 10⁻³]	<u>0.31</u>	Giraffe (n=9) and horses (n=5) over-represented in this model, so their data dominate.
	Time spent active (% day)	n _{studies} = 15 n _{species} = 3	-0.42 [-1.45, 0.62]	7.32 x 10 ¹²	Giraffe (n=9) and horses (n=5) over-represented in this model, so their data dominate. Other species present is cattle (n=1).
	Daily travel distance (km)	n _{studies} = 19 n _{species} = 6	-3.36 [-9.25, 1.89]	492.81	Giraffe (n=9) and horses (n=5) over-represented in this model, so their data dominate.
	Enclosure area (m ²)	n _{studies} = 11 n _{species} = 6	-3.16 x 10⁻³ [-11.19 x 10⁻³, 4.25 x 10⁻³]	4.84 x 10 ⁹	Three of the 11 studies have the same enclosure size (same zoo, in different years or with different animals).

Effect estimates and credible intervals (CrIs) for variables that correlated with stereotypy prevalence are shown in bold. Where a trend towards a correlation was found, CrIs are shown in italics. Bayes factors compare models with a null model containing only phylogenetic information and study as a random factor. A Bayes factor < 1 indicates that the model is no better at describing the data than the null model (underlined in table).

Table S5. Desirable attributes of zoo and livestock behaviour and welfare studies, to allow for more effective inter- and intra-species welfare comparisons in the future. We propose that studies should aim to meet as many of these criteria as conceivable, although we appreciate that it will not always be possible to meet them all. Where it is not possible to include the information listed in this table within the manuscript itself, it should be placed within online supplementary material, and signposted within the manuscript.

Category	Information needed	Detail required	Reason why
Subjects	Individual IDs	Names (zoo or equine studies) or location and dates of data collection (livestock)	Ensures data independence when compiling data from multiple studies.
	Sexes	Provide for each individual, wherever possible	Males and females behave differently, and understanding sex differences is important for assessing welfare.
	Breeding status	<ul style="list-style-type: none"> • Are animals used for breeding? • Are animals castrated? 	This information can then be included in intra- and inter-species comparisons of welfare
	Ages	Provide for each individual, wherever possible	Allows age to be used as a random factor in intra- and inter-species comparisons
	Location	Name and location of farm, yard, zoo, etc.	Ensures data independence, and allows the use of location as a random factor in analyses
	Diet	<ul style="list-style-type: none"> • <i>What</i> animals are fed • <i>When</i> they are fed 	This information can then be included in intra- and inter-species comparisons of welfare
	Enclosure	<ul style="list-style-type: none"> • Dimensions/sizes of both indoor and outdoor areas • Describe/list key features (water features, substrates, topography, flora, rooved/covered areas, etc.). A diagram would be beneficial here. • Any enclosure rotation protocols • Where daytime and night-time enclosures differ, give details of both 	This information can then be included in intra- and inter-species comparisons of welfare
	Enrichment	<ul style="list-style-type: none"> • <i>What</i> enrichment is given • <i>When</i> is it given (e.g. once a week, daily, etc.) • Give a rough idea of what behaviours the enrichment targets (e.g. feeders to encourage natural foraging) 	This information can then be included in intra- and inter-species comparisons of welfare
	Group information	<ul style="list-style-type: none"> • How many in group • Relationship to each other • Include animals not used for data collection • Where groups change overnight or during certain parts of the year (e.g. males kept separately) 	This information can then be included in intra- and inter-species comparisons of welfare
Early life information	<ul style="list-style-type: none"> • Age of weaning • Weaning method 	This information can then be included in intra- and inter-species comparisons of welfare	

		<ul style="list-style-type: none"> • Castration age • Castration method • Notes on any other early life trauma (such as in many sanctuary/rescue animals) • We appreciate this information is often not known/available, but it should be reported whenever it is. 	
Sampling and methods	High quality ethogram	<ul style="list-style-type: none"> • Clear, accurate definitions • If behaviours are excluded as not seen (e.g. stereotypic behaviours), note this. 	Those conducting intra- and inter-species comparisons can accurately assess the quality of the study and are able to cross-reference definitions between studies
	Stereotypic behaviour	<ul style="list-style-type: none"> • Clear definition of stereotypic behaviour being worked to (we strongly suggest the use of Mason's definition from 2007 (22)). • As a minimum, separate SBs by type (oral, locomotor, and other) rather than lumping them all together • Where possible, also describe each individual SB seen • Give data on both the prevalence of SB across the population, and the time spent performing SB (average proportion of time budget for stereotyping animals only). These should be separated by type. 	Those conducting intra- and inter-species comparisons can accurately assess and categorise SB, are able to cross-reference definitions between studies, and determine whether the data collected meets their inclusion criteria
	Sampling	<ul style="list-style-type: none"> • Type of sampling used (scan or focal) • Frequency of sampling • Length of watches/sampling bouts • Was sampling live or from recordings 	Those conducting intra- and inter-species comparisons can accurately assess whether the data collected meets their inclusion criteria
	Dates of data collection	Specific dates, or a range (e.g. Feb – April 2021) if data were collected over a longer period of time	Ensures data independence when compiling data from multiple studies.
	Minimum 48hrs of observations	Wherever possible, behavioural observations should be taken over a minimum of 48 hours, and ideally longer and repeated at several timepoints over a year	Short periods of data collection produce less valid data due to natural variation in behaviour
	Baseline data	In modification studies (e.g. when testing the effect of a new diet on behaviour) ensure that baseline data is collected over a sufficient period to provide valid data. Minimum 48hours (see above).	Short periods of data collection produce less valid data due to natural variation in behaviour
Results	Raw data	<ul style="list-style-type: none"> • Provide data for each individual, as well as averages (this can go in supplementary material) • Ensure this is provided alongside the subject information listed above • Signpost where this data can be found within the manuscript 	Allows data for each individual to be included in cross-species analyses, rather than having to use averages across populations/species
	Sex disaggregated	<ul style="list-style-type: none"> • Esp. important if data for individuals cannot be given (e.g. in it was not possible to ID individuals during sampling) 	Males and females behave differently, and understanding sex differences is important for assessing welfare.

		<ul style="list-style-type: none"> Give averages of behaviour or welfare measures for the two sexes separately, as well as providing overall averages 	
	Behaviours not seen	If a behaviour was not seen, make a note of this	Which behaviours are absent is just as important as knowing which are present, when assessing welfare.

Dataset and R script legends

Dataset S1 (separate file accessible via OSF at <https://osf.io/mkcw8/>). Compiled stereotypy and wild behavioural biology data for captive ungulate species. Coding information is available on the second sheet of the file.

Dataset S2 (separate file accessible via OSF at <https://osf.io/mkcw8/>). Full text screening of stereotypic behaviour sources.

Dataset S3 (separate file accessible via OSF at <https://osf.io/mkcw8/>). Full text screening of wild behavioural biology sources.

Dataset S4 (separate file accessible via OSF at <https://osf.io/mkcw8/>). Phylogenetic tree of ungulate species for which stereotypy data were available.

R Script S1 (separate file accessible via OSF at <https://osf.io/mkcw8/>). Brm modelling of stereotypy prevalence (%).

R Script S2 (separate file accessible via OSF at <https://osf.io/mkcw8/>). Brm modelling of stereotypy prevalence (%) without the inclusion of intensively reared livestock.

R Script S3 (separate file accessible via OSF at <https://osf.io/mkcw8/>). Brm modelling of time spent performing oral stereotypy (%).

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