

**Research article** 

# Body mass of adult zoo hippos (Hippopotamidae) and how they compare to data from populations in the wild

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#### Abstract

The body mass of zoo animals is a strong indication of the life conditions they receive under human care and how they adapt to them. Hippopotamuses (Hippos) in zoos are often considered overweight, but a comparison between the body mass of wild populations and the zoo population has never been done before. Here, we analysed the records of adult body mass of the global zoo populations of hippos (Hippopotamus amphibius and Choeropsis liberiensis) and compared them with available field data from wild populations found in the literature. Furthermore, we analysed trends in body mass with age and seasonality. Zoo hippos of both species are on average heavier than their wild counterparts. This disparity is of greater extent in pygmy hippos than in common hippos, and it can be visually attested when comparing body condition on photographs of zoo and free-ranging individuals. Both zoo populations display sexual body mass dimorphism, with adult males being on average heavier than adult females. For common hippos, this sexual dimorphism is much more prominent in the zoo population than in wild populations, possibly due to males having the full nutritional potential to grow to larger sizes in zoos. Neither species displays consistent seasonal fluctuations in body mass, contrary to what is described for common hippos in the wild due to fluctuations in the availability of resources. While no immediate population-level health problems seem to be prevalent in either species due to overweight, it nevertheless might hinder the management and breeding of these two endangered species due to high infant mortality and earlier puberty. Changes in zoo hippo nutrition should aim to adjust body mass and body condition to values similar to those observed in wild populations by offering them an appropriate diet and monitoring body condition. Our results also demonstrate that efforts to improve nutrition in the last decade have yielded a positive trend of body mass reduction in pygmy hippos in zoos.

## Introduction

Zoo-housed animals are frequently described as being larger and heavier than their free-ranging counterparts (Schwitzer and Kaumanns 2001; Garand et al. 2024) and obesity is a common pathology (Videan et al. 2007). This problem is linked to the overfeeding of individuals with energy-dense and often inappropriate foods (Clauss et al. 2009; Heidegger et al. 2016) and lack of activity (Tang et al. 2023). Furthermore, obesity in zoo animals has been linked to health problems such as cardiovascular diseases (Ely et al. 2013), diabetes (Kuhar et al. 2013), musculoskeletal problems (Heidegger et al. 2016) and even impaired reproductive function (Freeman et al. 2009; Edwards et al. 2015; Morfeld and Brown 2016).

Hippopotamuses (hereafter termed hippo(s)) are large semi-aquatic herbivores from the riverine habitats of sub-Saharan Africa. The diet of the common hippo *Hippopotamus amphibius* consists mainly of grasses, with only a rare inclusion of fruits, woody vegetation, aquatic plants, and even less frequently meat obtained from scavenging (Bere 1959; Dudley et al. 2016; Voysey et al. 2023). Wild populations of common hippos are often exposed to large seasonal variations in food availability, impacting their body condition (Chomba 2013). Pygmy hippo *Choeropsis liberiensis* feeding habits have been scarcely studied in the wild, but they have been described as intermediate generalist herbivores, feeding from a wide range of plant species, mostly grasses but including shrubs and ferns (Hendier et al. 2021).

In zoos, it has been described that hippos are prone to suffer from excessive weight (Schwarm et al. 2006; Taylor et al. 2013; Miller et al. 2014). This issue is attributed to the oversupply of a nutrient-dense diet, comparatively low metabolic rates (Schwarm et al. 2006), and the lack of exercise in zoos (Tennant et al. 2018). Nevertheless, so far, no comparative data exist on the body weights of wild hippo populations and zoo hippos. Weight management and monitoring have become a fundamental pillar of zoo animal nutrition, health, and welfare (Clavadetscher et al. 2021). Assessing the body mass of free-ranging populations provides a range of reference values that can be seen as acceptable for the biology and health of the species. By comparing the body mass of zoo animals with these reference values, an appropriate weight management plan can be defined for those individuals who deviate from the reference values.

In order to assess the extent to which the body mass of zoomanaged hippos deviates from that reported for their free-ranging conspecifics, we compared data collected from the global zoo community via the Species360 database with published literature reports.

#### Methods

As part of Species360 research data use agreement # 84212, we received data on body masses of hippos recorded in the Zoo Information Management System (ZIMS) and stored by Species360 in January 2022 (Table 1). The data was anonymised, indicating only the body mass entered by a zoo and the corresponding age of the animal, but not the identity or the latitude of the reporting zoo. Additionally, the data did not include an indication of the reproductive status of individuals (e.g., whether animals were pregnant), and an effect of pregnancy on potential body mass fluctuations therefore could not be controlled for. These raw data were provided with an indication of which data points were considered outliers by several automated correction procedures inspired by Garand et al. (2024). These included the automatic flagging of entries above 7000 kg, of outliers based on percentiles of a sliding window along the age for juveniles and adults, of

outliers based on the residuals of generalized additive models for each individual trajectory with at least 7 measurements, and of outliers based on the residuals of a common generalized additive model for all growth trajectories. Based on visual judgement, these procedures removed the majority of outliers from the dataset. However, some evident outliers still remained (for example, if an outlier occurred in a sliding window with very few measurements and hence biologically implausibly wide percentiles), which were removed manually from the datasets.

For each species, for females and males separately, a Gompertz growth model was fitted to the data. This model yields an asymptotic weight which can be interpreted as the growth plateau (Zullinger et al. 1984). Note that Gompertz models need not necessarily be the best models to fit growth data (reviewed in Veylit et al. (2021)); here, we did not employ them to yield the most accurate data fit, but only to define the age at which animals typically reach adult size. The adequacy of the models was checked by inspecting the resulting model as graphed against the raw data (Figure S1). We defined the age from which on data would be included in the calculation of an adult average as that when 95% of this asymptotic mass was reached. The resulting parameter estimates and ages used as the cut-off to define adulthood size are given in Table 1.

Body mass was first averaged per individual (using only data above the adulthood cutoff), and then across the means of all individuals. After confirming the normal distribution of the sex-specific body mass data of males and females using the Shapiro-Wilk normality test, we tested for sexual dimorphism in the zoo population by an independent t-test in case p(Shapiro-Wilk)>0.05, and otherwise by a Mann-Whitney-U test using python's scipy package. Next, we calculated the average of all adult individuals weighed in a year and displayed the resulting averages for a pattern (increase or decrease) from the first year onwards for which data from at least 10 individuals were available. The average age of these animals was equally plotted to assess potential age-dependent effects. Additionally, two patterns were assessed visually by analysing the data for each individual animal separately: (i) regular, annual (i.e., seasonal) fluctuations in body mass, and (ii) a decrease in body mass towards later adult life. As a first step, only those individuals were selected for which at least three measurements in both, the first part of the expected lifetime as well as the second part of the expected lifetime were present.

**Table 1.** Results of Gompertz model fit (according to  $y=A e^{-k(t+1)}_{0}$ ) to the age-specific body mass data of females and males of hippo species kept in zoos, and the resulting threshold age for defining adulthood. A=asymptotic adult body mass; k=relative growth rate;  $t_0$ =time until maximum growth.

Species	Sex	Asymptote mass (A; kg)	Time to maximum growth (t <sub>o</sub> , years)	Relative growth rate (k; d <sup>-1</sup> )	Threshold age (years)
Choeropsis liberiensis	Female	248.3±0.75	2.74±0.06	0.82±0.02	4.83
	Male	264.62±0.77	2.90±0.08	0.92±0.02	4.38
Hippopotamus amphibius	Female	1482.78±3.48	2.53±0.06	0.46±0.01	8.39
	Male	1679.93±6.79	3.04±0.13	0.53±0.02	7.73

To assess seasonal fluctuations, pairs of measurements between one winter and the subsequent summer (or vice versa) were used. All measurements per such a season were averaged and corrected for the age-trend. Afterwards, each pair was assigned a score (+1, 0, or -1) which signifies whether this corrected value was larger during summer, the same up to 0.5% between summer and winter, or larger during winter. The average over the scores per pair yields an intuitive measure of a seasonality strength (-1 winter is larger than summer, 0 no difference, +1 summer is larger than winter). A seasonality effect was suspected if this absolute score exceeded 0.3 and the score was built on at least six summer/ winter pairs. Finally, the data of these pre-selected individuals were plotted and all inspected individually, assessing subjectively if the detected pattern was visually evident (then it was counted) or not (then it was not). An example of such an individual plot is given in Figure S2. Using this information, we determined the proportion of individuals that showed a seasonally fluctuating body mass. Similarly, we assessed whether there was a decline in body mass with progressing age late in adult life.

Data on the body mass of free-ranging hippos were taken from the scientific literature (Table 2).

### Results

Sources for the body weight of wild pygmy hippos are very scarce with only a few measurements cited by Flacke et al. (2015). Two adult female specimens were weighed in the Taï National Park with 165 and 170 kg, while one male shot in Nigeria had 204 kg (Table 2).

Amongst wild adult common hippos, the mean body mass was 1315.76 ( $\pm$ 172.1) kg for females and 1354.19 ( $\pm$ 246.8) kg for males, as derived from data collected by Richard Laws in the Queen Elizabeth Park, Uganda, between 1961 and 1966 (Shannon et al. 2021) (Table 2). Note that in the dataset provided by Shannon et al. (2021), we considered that animals reached their adult size at 8 years of age, according to the Gompertz Model we applied to our zoo hippo dataset (Table 1), while the authors considered adult size hippos from 10 years of age onwards. It is also worth noting that such a large sample size and age data like those of the wild common hippo dataset (Shannon et al. 2021) are not common in most cases of wild fauna field data. Shannon et al. (2021) found that adult ( $\geq$ 10 years old) males are 5% heavier on average than females.

Bere (1959), also in the Queen Elizabeth Park, noted that the heaviest individual was a female above 2000 kg and that males were on average heavier than females (Table 2). However, Bere considered the hippos in this location to be lighter and slimmer than what is typical for common hippos: "Accurate comparative weights of hippos from other parts of Africa are not available to me, but the Queen Elizabeth Park hippos may well be lighter than average, a circumstance resulting from the poor grazing. Very few of the animals examined carried much sub-cutaneous fat" (Bere 1959).

For the global zoo population of pygmy hippos, the manually corrected dataset contained 81 female and 57 male individuals (Table 3). The average body mass of zoo-kept animals was 240.44 ( $\pm$ 31.7) kg for females and 251.25 ( $\pm$ 32.62) kg for males (Table 3). Males are significantly heavier than females (4.5% on average) -

Table 2. Body mass records (in kg) for adult, free-ranging hippos in natural habitats

Source	n	minimum	average	maximum
Choeropsis liberiensis				
Females				
Heslop (1944) as cited by Flacke et al. (2015)	2	165	167.5±2.5	170
Males				
Hentschel (1990) as cited by Flacke et al. (2015)	1	-	204	-
Hippopotamus amphibius				
Females				
Shannon et al. (2021) * (data from Laws in Queen Elizabeth Park, Uganda 1961-1966)	638	773	1316±172	1794
Bere (1959) (data from Longhurst in Queen Elizabeth Park, Uganda, 1958)	171		1362	2020
Males				
Shannon et al. (2021) * (data from Laws in Queen Elizabeth Park, Uganda 1961-1966)	439	701	1354±247	2065
Bere (1959) (data from Longhurst in Queen Elizabeth Park, Uganda, 1958)	273		1477	1898

\*Values here displayed are limited to the adult size age defined by the Gompertz growth model=8 years of age (Table 1).

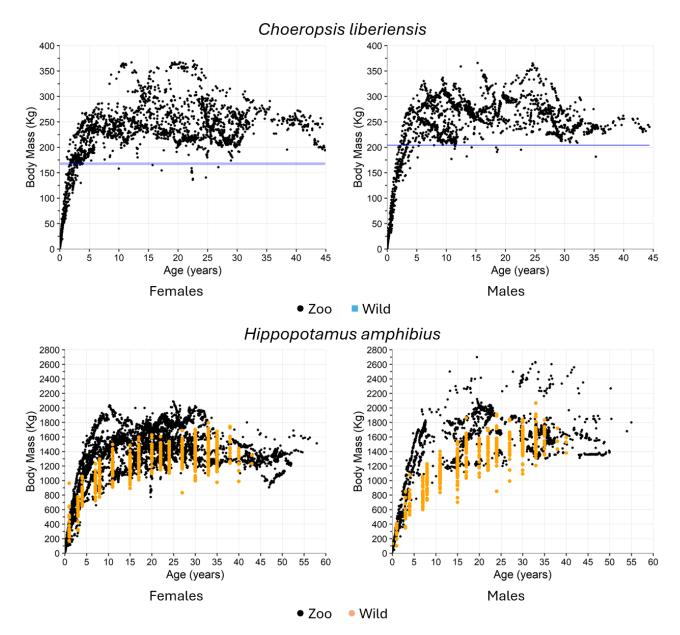


Figure 1. Body mass data for zoo-kept hippo species (black dots) as compared to the literature data range of adult, free-ranging specimens (blue in *C. liberiensis* and orange in *H. amphibius*) (for sources, see Table 2). Note that this selection of individuals is based on data availability and not necessarily representative for the current global zoo populations.

Table 3. Body mass records (in kg) and patterns for adult, zoo-kept hippo species. Note that this selection of individuals is based on data availability and not necessarily representative for the current global zoo populations.

Sex	n	mean±SD (min, max)	% seasonal fluctuations (of n)	% old age decline (of n)
Choeropsis liberiensis				
Female	81	240.4±31.7 <sup>A</sup> (153.3, 335.1)	12.5% (16)	84.6% (13)
Male	57	251.3±32.6 <sup>B</sup> (181.4, 333.4)	0% (9)	100% (6)
Hippopotamus amphi	bius			
Female	94	1461±253° (880, 2040)	0% (14)	54.5% (11)
Male	54	1750±351⁵ (1015, 2845)	0% (6)	57.1% (7)

AB, ab indicate significant sexual dimorphism, as assessed by parametric t-test (<sup>A,B</sup>) or nonparametric U-test (<sup>a,b</sup>) in the case of not normally distributed data.

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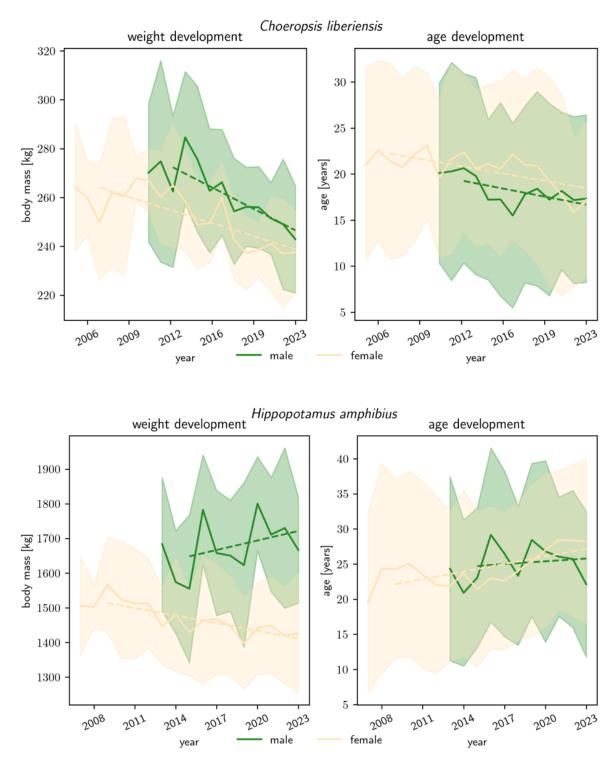




Figure 2. Historical trends (by year) in mean body mass (left) and age (right) of adult zoo-kept hippos. Medians were used from the first year where a minimum of 10 individuals were present in the dataset. Note that this selection of individuals is based on data availability (individuals weighed) and not necessarily representative of the current global zoo populations.

the number of individuals and the descriptive statistics are given in Table 3. Averages for both sexes are well above the few recorded body masses of wild specimens (Figure 1).

For the common hippo zoo population, the manually corrected dataset contained 94 female and 54 male individuals (Table 3). The

average body mass of zoo-kept animals was 1461.19 ( $\pm$ 253.31) kg for females and 1750.2 ( $\pm$ 351.06) kg for males (Table 3). With this difference between sexes being significant, adult males are almost 20% heavier on average than adult females (Table 3). Adult animals in zoos are 145 kg (11.1%) and 396 kg (29.2%) heavier



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Figure 3. Comparison of body condition between free-ranging (left column) and high body condition zoo (right column) pygmy hippos Choeropsis liberiensis.

on average than adult female and male animals in the wild, respectively (Figure 1).

Regarding seasonal fluctuations of body mass, none of the two species consistently displayed a seasonal variation pattern in body mass (Table 3). Both species displayed a decline in mass with advanced age to variable extents. This is very marked in pygmy hippos, with almost all individuals displaying a decline with age (between 84.6 to 100% of the assessed individuals). In common hippos, only a small majority of animals (54.5 to 57.1%) have a consistent reduction in body mass over their later lifespan (Table 3).

Assessing the historical trend in the population's body mass, we observe that, on average, pygmy hippos' mass has declined in the last decade, and this was not due to an average increase in age in this population – on the contrary (Figure 2). Regarding common hippos, the body mass of the females has declined, and the body mass of males has risen over time while the average age of the weighed animals has slightly increased (Figure 2).



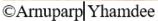


Figure 4. Zoo pygmy hippos Choeropsis liberiensis in "good" body condition



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## Discussion

Zoo animal nutrition has been receiving increasing attention in the last decades, as it has been linked to health and welfare issues and also to poor reproductive performance (Freeman et al. 2009; Edwards et al. 2015; Morfeld and Brown 2016; Fens and Clauss 2024). These impacts are even more significant when referring to breeding programmes of endangered species and their long-term sustainability. Being threatened in the wild, the zoo populations of both hippo species can offer vast contributions to the conservation of wild populations (Farhadinia et al. 2020). Therefore, it is important to guarantee optimal health, welfare and breeding outcomes for the individuals. To the best of our knowledge, body condition has only been linked to breeding problems in pygmy hippos, and has not yet been reported for common hippos. The obesity of many breeding females may be influencing the number of stillbirths or other perinatal mortality causes, which are still considered too high in this species' breeding programme (Flacke et al. 2016).

For pygmy hippos, the discrepancy between the body mass observed in zoos and those recorded in the wild is large. Even a visual comparison of photographs from wild specimens with those from zoos often reveals that the body condition of zoo animals is very variable (Figures 3 and 4), with many individuals in zoos being too high in body condition (Taylor et al. 2013) (Figure 3). These findings raise concerns regarding the nutritional adequacy and composition of the diets provided to the species, and the extent to which enclosure design in zoos facilitates species-appropriate levels of physical activity.

Common hippos in zoos are on average heavier than their wild counterparts, but with a smaller discrepancy than that observed for pygmy hippos (Figure 1). Notably, Bere (1959) suspects that hippos in Queen Elizabeth Park were smaller and lighter than expected for the species - which might mean that an even smaller discrepancy between zoo and wild animals is possible. We do not have data to disclaim or support his statement. Nevertheless, there is a large overlap between body masses observed in zoo and free-ranging common hippos (Figure 1), suggesting that the frequency of overweight or obese animals in zoos is likely not as prevalent as for pygmy hippos.

In our data, male zoo common hippos were considerably heavier than females. Common hippos in the wild show minor sexual dimorphism in their body mass, with only the weight of canines and jaws being considerably larger in males than in females (Shannon et al. 2021). Dinerstein (1991) also described a much larger difference between adult male and female Indian rhinoceros *Rhinoceros unicornis* in zoos than what he found in wild populations, with wild adult males being just slightly larger than females, and the only conspicuous differences in the size of the dental weaponry (lower outer incisors) and musculature of the neck and shoulders. Possibly, the high resource availability in zoos, where food is constantly available, allows males to grow to their full potential.

To our knowledge, there are no health issues associated with obesity in common hippos. However, body mass and puberty have been strongly linked in zoo common hippos (Wheaton et al. 2006). Increased body weight might trigger puberty in young female hippos earlier than expected, just as it happens with humans (Biro et al. 2012) and zoo elephants (Glaeser et al. 2012), resulting in undesired and early pregnancies.

Neither zoo hippo species showed consistent seasonal fluctuations in body mass. Again, this is mostly likely due to the constant supply of food across the year. By contrast, common hippos in the wild experience seasonal fluctuations in body condition, reflecting the seasonal variations in the supply of pasture seen in tropical savannas (Chomba 2013). Hippos have been described as having low metabolic rates (Schwarm et al. 2006). This is possibly an adaptation to their peculiar lifestyle, but it is the perfect recipe for obesity when living with a stable food supply and stable climatic conditions such as in zoos.

Age-related body mass senescence has been described in many mammal species - for instance, mice (Hamrick et al. 2006), lemurs (Hämäläinen et al. 2014), marmots (Tafani et al. 2013; Kroeger et al. 2018), ruminants (Weladji et al. 2010; Nussey et al. 2011; Douhard et al. 2017) and humans (Forbes and Reina 1970). The reduction in body mass has been linked to loss of muscle (lean) mass in old age in a process called sarcopenia (Demontis et al. 2013) and with a reduction in bone density due to a reduction of activity levels (Hamrick et al. 2006). Our results demonstrate that both hippos follow, to a different extent, a similar pattern of body mass decline with advancing age. Loss of body mass with age, however, increases the risk of obesity, since it is often followed by a decrease in muscle(lean):fat ratios, activity levels and reduced metabolic rate, as described for humans and dogs (Harper 1998). Thus, with advancing age, it becomes even more relevant to do a correct management and monitoring of body condition/mass and diet for hippos in zoos.

We cannot tell if body mass senescence is unique to zoo hippos, but most certainly it also occurs in wild populations, since most of the examples in the literature (listed previously) refer to freeranging populations. The exception is Hämäläinen et al. (2014) which examined one captive and two wild populations of lemur *Microcebus murinus*. Their results showed that a decline in body mass with age was only observed in captive animals due to intrinsic factors such as reduced activity, loss of lean mass and bone density. They hypothesize that in the wild, lighter individuals are less fit and are the first ones to be removed from the population via predation – something that does not occur in the captive setting.

Considerable modifications to pygmy hippo diets can improve the body condition of individuals considered obese (Taylor et al. 2013) and keeping individuals in acceptable body conditions is possible (Figure 4). In the case documented by Taylor et al. (2013), a male pygmy hippo was considered obese at about 280 kg and stabilized after a diet change at 230-240 kg. Our results demonstrate that the average body mass of zoo pygmy hippos has decreased in the last 20 years of husbandry for this species at a very similar magnitude (Figure 2). This is mostly likely due to the increased collective effort in improving the husbandry for this species (Meireles et al. 2025), further supported by the regular publication of updated husbandry guidelines (von Houwald et al. 2020).

The true paradigm in zoo animal nutrition is the urge to abandon outdated practices and adjust husbandry routines to those that more closely offer the animals the nutritional conditions they face in their natural environments (Fens and Clauss 2024). For hippos, this translates to the total elimination of any cultivated fruits, starchy vegetables or any highly digestible, high-starch pelleted feeds and instead the provision of high-quality roughage (Schwarm et al. 2006) as well as facilitating their feeding habits – nocturnal terrestrial grazing (Tennant et al. 2018). The development of body condition scores for each species facilitates the monitoring by the animal care staff when other tools are not easily available, namely a scale or if the animals are not trained for routine weighing (Clavadetscher et al. 2021). Published cases (Taylor et al. 2013) prove that improving hippo diets to achieve better body conditions is possible.

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### References

Bere R. (1959). Queen Elizabeth National Park: Uganda the hippopotamus problem and experiment. *Oryx* 5(3): 116–124.

- Biro F.M., Greenspan L.C., Galvez M.P. (2012) Puberty in girls of the 21st century. Journal of Pediatric and Adolescent Gynecology 25(5): 289– 294.
- Chomba C. (2013) Factors affecting the Luangwa (Zambia) hippo population dynamics within its carrying capacity band–insights for better management. *International Journal of Biodiversity and Conservation* 5(3): 109–121.
- Clauss M., Wilkins T., Hartley A., Hatt J.-M. (2009) Diet composition, food intake, body condition, and fecal consistency in captive tapirs (*Tapirus* spp.) in UK collections. *Zoo Biology* 28(4): 279–291.
- Clavadetscher I., Bond M., Martin L., Schiffmann C., Hatt J.M., Clauss M. (2021) Development of an image-based body condition score for giraffes *Giraffa camelopardalis* and a comparison of zoo-housed and free-ranging individuals. *Journal of Zoo and Aquarium Research* 9(3): 170–185.
- Demontis F., Piccirillo R., Goldberg A.L., Perrimon N. (2013) Mechanisms of skeletal muscle aging: insights from Drosophila and mammalian models. *Disease Models & Mechanisms* 6(6): 1339–1352.
- Dinerstein E. (1991) Sexual dimorphism in the greater one-horned rhinoceros (*Rhinoceros unicornis*). *Journal of Mammalogy* 72(3): 450–457.
- Douhard F., Gaillard J.M., Pellerin M., Jacob L., Lemaître J.F. (2017) The cost of growing large: Costs of post-weaning growth on body mass senescence in a wild mammal. *Oikos* 126(9): 1329–1338.
- Dudley J.P., Hang'Ombe B.M., Leendertz F.H., Dorward L.J., de Castro J., Subalusky A.L., Clauss M. (2016) Carnivory in the common hippopotamus *Hippopotamus amphibius*: implications for the ecology and epidemiology of anthrax in African landscapes. *Mammal Review* 46(3): 191–203.
- Edwards K.L., Shultz S., Pilgrim M., Walker S.L. (2015) Irregular ovarian activity, body condition and behavioural differences are associated with reproductive success in female eastern black rhinoceros (*Diceros bicornis michaeli*). *General and Comparative Endocrinology* 214: 186– 194.
- Ely J.J., Zavaskis T., Lammey M.L. (2013). Hypertension increases with aging and obesity in chimpanzees (*Pan troglodytes*). *Zoo Biology* 32(1): 79– 87.
- Farhadinia M.S., Johnson P.J., Zimmermann A., McGowan P.J., Meijaard E., Stanley-Price M., Macdonald D.W. (2020) Ex situ management as insurance against extinction of mammalian megafauna in an uncertain world. *Conservation Biology* 34(4): 988–996.
- Fens A., Clauss M. (2024) Nutrition as an integral part of behavioural management of zoo animals. *Journal of Zoo and Aquarium Research* 12(4): 196–204.
- Flacke G.L., Chambers B.K., Martin G.B., Paris M.C. (2015) The pygmy hippopotamus *Choeropsis liberiensis* (Morton, 1849): Bringing to light research priorities for the largely forgotten, smaller hippo species. *Der Zoologische Garten* 84(5–6): 234–265.
- Flacke G.L., Tkalčić S., Steck B., Warren K., Martin G.B. (2016) A retrospective analysis of mortality in captive pygmy hippopotamus (*Choeropsis liberiensis*) from 1912 to 2014. *Zoo Biology* 35(6): 556–569.
- Forbes G.B., Reina J.C. (1970) Adult lean body mass declines with age: some longitudinal observations. *Metabolism* 19(9): 653–663.
- Freeman E.W., Guagnano G., Olson D., Keele M., Brown J.L. (2009). Social factors influence ovarian acyclicity in captive African elephants (*Loxodonta africana*). *Zoo Biology* 28(1): 1–15. https://doi.org/https:// doi.org/10.1002/zoo.20187
- Garand E., Krauss C., Müller D.W.H., Davis L.R., Codron D., Clauss M., Miranda F. (2024) Larger than life? Body mass records of zoo-managed giant anteaters (*Myrmecophaga tridactyla*). *Zoo Biology* 43(6): 537– 544. https://doi.org/10.1002/zoo.21865
- Glaeser S., Hunt K., Martin M., Finnegan M., Brown J. (2012) Investigation of individual and group variability in estrous cycle characteristics in female Asian elephants (*Elephas maximus*) at the Oregon Zoo. *Theriogenology* 78(2): 285–296.
- Hämäläinen A., Dammhahn M., Aujard F., Eberle M., Hardy I., Kappeler P.M., Perret M., Schliehe–Diecks S., Kraus C. (2014) Senescence or selective disappearance? Age trajectories of body mass in wild and captive populations of a small-bodied primate. *Proceedings of the Royal Society B* 281(1791): 20140830.
- Hamrick M.W., Ding K.H., Pennington C., Chao Y.J., Wu Y.D., Howard B., Immel D., Borlongan C., McNeil P.L., Bollag W.B. (2006) Age-related loss of muscle mass and bone strength in mice is associated with a decline in physical activity and serum leptin. *Bone* 39(4): 845–853. https://doi.org/10.1016/j.bone.2006.04.011

- Harper E.J. (1998) Changing perspectives on aging and energy requirements: aging, body weight and body composition in humans, dogs and cats. *The Journal of Nutrition* 128(12): 2627–2631. https:// doi.org/10.1093/jn/128.12.2627S
- Heidegger E.M., von Houwald F., Steck B., Clauss M. (2016) Body condition scoring system for greater one-horned rhino (*Rhinoceros unicornis*): Development and application. *Zoo Biology* 35(5): 432–443. https:// doi.org/10.1002/zoo.21307
- Hendier A., Chatelain C., Du Pasquier P.E., Paris M., Ouattara K., Koné I., Croll D., Zuberbühler K. (2021) A new method to determine the diet of pygmy hippopotamus in Taï National Park, Côte d'Ivoire. African Journal of Ecology 59(4): 809–825.
- Kroeger S.B., Blumstein D.T., Armitage K.B., Reid J.M., Martin J.G. (2018) Age, state, environment, and season dependence of senescence in body mass. *Ecology and Evolution* 8(4): 2050–2061.
- Kuhar C., Fuller G., Dennis P. (2013) A survey of diabetes prevalence in zoo-housed primates. *Zoo Biology* 32(1): 63–69.
- Meireles J.P., Scherer L., Bingaman Lackey L., Steck B., Pluháček J., Roller M., Müller D.W.H., Bertelsen M.F., Clauss M. (2025) Historical survivorship and demographic structure of zoo-housed hippos (Hippopotamidae). *Journal of Zoo and Aquarium Research*, (in press) 13(2):.
- Miller M., Fleming G.J., Citino S.B., Hofmeyr M. (2014) Hippopotamidae. In: West G., Heard D., Caulkett N. (eds.). *Zoo Animal and Wildlife Immobilization and Anesthesia*, Second Edition. Ames, IA: Wildey Blackwell, 787–795.
- Morfeld K.A., Brown J.L. (2016) Ovarian acyclicity in zoo African elephants (*Loxodonta africana*) is associated with high body condition scores and elevated serum insulin and leptin. *Reproduction, Fertility and Development* 28(5): 640–647.
- Nussey D.H., Coulson T., Delorme D., Clutton-Brock T.H., Pemberton J.M., Festa-Bianchet M., Gaillard J.M. (2011) Patterns of body mass senescence and selective disappearance differ among three species of free-living ungulates. *Ecology* 92(10): 1936–1947.
- Schwarm A., Ortmann S., Hofer H., Streich W.J., Flach E., Kühne R., Hummel J., Castell J., Clauss M. (2006) Digestion studies in captive Hippopotamidae: a group of large ungulates with an unusually low metabolic rate. *Journal of Animal Physiology and Animal Nutrition* 90(7-8): 300–308.
- Schwitzer C., Kaumanns W. (2001) Body weights of ruffed lemurs (Varecia variegata) in European zoos with reference to the problem of obesity. Zoo Biology 20(4): 261–269.

- Shannon G., Sadler P., Smith J., Roylance-Casson E., Cordes L.S. (2021) Contrasting selection pressure on body and weapon size in a polygynous megaherbivore. *Biology Letters* 17(10):https://doi. org/10.1098/rsbl.2021.0368
- Tafani M., Cohas A., Bonenfant C., Gaillard J.M., Lardy S., Allainé D. (2013) Sex-specific senescence in body mass of a monogamous and monomorphic mammal: the case of Alpine marmots. *Oecologia* 172: 427–436.
- Tang Y., Jia T., Zhou F., Wang L., Zhang L. (2023) Obesity status and its relative factors of captive Asian elephants (*Elephas maximus*) in China based on body condition assessment. *bioRxiv*: 2023–2011.
- Taylor L.A., Rudd J., Hummel J., Clauss M., Schwitzer C., Steck B. (2013) Weight loss in pygmy hippos (*Choeropsis liberiensis*). In: Steck, B. *International Studbook for the Year 2012 - Pygmy Hippopotamus*. Basel, CH: Zoo Basel, 20–25.
- Tennant K.S., Segura V.D., Morris M.C., Snyder K.D., Bocian D., Maloney D., Maple T.L. (2018) Achieving optimal welfare for the Nile hippopotamus (*Hippopotamus amphibius*) in North American zoos and aquariums. *Behavioural Processes* 156: 51–57.
- Veylit L., Sæther, B.E., Gaillard J.M., Baubet E., Gamelon M. (2021) Many lifetime growth trajectories for a single mammal. *Ecology and Evolution* 11(21): 14789–14804.
- Videan E.N., Fritz J., Murphy J. (2007) Development of guidelines for assessing obesity in captive chimpanzees (*Pan troglodytes*). *Zoo Biology* 26(2): 93–104.
- von Houwald F., Wenker C., Flacke G., Steck B., Osterballe R., Viduna R., Schmidt F., Matthews A. (2020) *EAZA Best Practice Guidelines* for the Pygmy Hippopotamus (Choeropsis liberiensis): 1st Edition, Amsterdam, NL: European Association of Zoos and Aquaria.
- Voysey M.D., de Bruyn P.N., Davies A.B. (2023) Are hippos Africa's most influential megaherbivore? A review of ecosystem engineering by the semi-aquatic common hippopotamus. *Biological Reviews* 98(5): 1509–1529.
- Weladji R.B., Holand Ø., Gaillard J.M., Yoccoz N.G., Mysterud A., Nieminen M., Stenseth N.C. (2010) Age-specific changes in different components of reproductive output in female reindeer: terminal allocation or senescence? *Oecologia* 162: 261–271.
- Wheaton C.J., Joseph S., Reid K., Webster T., Richards M., Savage A. (2006) Body weight as an effective tool for determination of onset of puberty in captive female Nile hippopotami (*Hippopotamus amphibius*). *Zoo Biology* 25(1): 59–71.
- Zullinger E.M., Riclefs R.E., Redford K.H., Mace G.M. (1984) Fitting sigmoidal equations to mammalian growth curves. *Journal of Mammalogy* 65(4):, 607–636.