

DER ZOOLOGISCHE GARTEN

THE ZOOLOGICAL GARDEN

Zeitschrift für die gesamte Tiergärtnerei (Neue Folge)



Offizielles Organ des Verbandes der Zoologischen Gärten – VdZ
Organ of the World Association of Zoos and Aquariums – WAZA



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Volume 91 · 2023

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VNW

Verlag Natur & Wissenschaft · Solingen

DER ZOOLOGISCHE GARTEN

doi:10.53188/zg0011

Zool. Garten N.F. 91 (2023) 1-7

THE ZOOLOGICAL GARDEN

Non-invasive reproductive monitoring in round-eared elephant shrews (*Macroscelides proboscideus*)

Nicht-invasives Monitoring von Sexualhormonmetaboliten bei Kurzohrrüsselspringern (*Macroscelides proboscideus*)

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Abstract

Breeding elephant shrews is difficult and few is known about their sexual cycle and their reproduction biology. Therefore, fecal estrogen and progesterone metabolite excretion was monitored in round-eared elephant shrews (*Macroscelides proboscideus*) (n=6) for up to four months. Daily fecal samples were collected and analyzed using enzyme immunoassays (EIA) for estrogen and progesterone metabolites. The female elephant shrews monitored in this study showed a variable cycle length of 6-31 days with an average cycle length of 15.5 days. Females with visual and olfactory contact with males had a shorter cycle length (average of 11.5 and 13 days) and higher progesterone metabolite values than females without contact with males. Due to this observation, we hypothesize that female round-eared elephant shrews have induced ovulation. Because of missing periodic variations in the progesterone concentrations, only estrogen can be used for non-invasive estrous cycle diagnostic in round-eared elephant shrews. Due to the small sample size in this study (n=6), further research is necessary.

Keywords: round-eared elephant shrew, *Macroscelides proboscideus*, reproduction biology, sexual cycle

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Introduction

The insectivorous elephant shrews or sengis belong to the mammalian clade *Afrotheria* (Rathbun, 2009). Within this clade, the order of the *Macroscelidea* contains one family (*Macroscelididae*) with four genera, which, depending on the author, comprise 15–17 species (Rathbun, 2009; Rudloff, 2009; Westheide & Rieger, 2015). Except for *Elephantulus rozeti*, the only species in northern Africa, the elephant shrews' distribution is restricted to the southern half of Africa (Douady, 2003).

The most common sengi in captivity is the round-eared elephant shrew (*Macroscelides proboscideus*). Its cute appearance and high activity rate make this species one of the most popular small mammals in zoological collections (Olbricht & Sliwa, 2010; Rudloff, 2009; Zootierliste, 2019). According to the literature, the estrus cycle of this monogamous species varies from 14 days to 2.5 months (Rudloff, 2009; Schubert, 2009). This study aimed to specify the female sexual cycle via non-invasive fecal hormone monitoring, a standard method used for endocrine analysis in many wildlife species (Schwarzenberger & Brown, 2013). Due to numerous confusions in sexing elephant shrews (Sicks, personal communication), we further aimed to develop a non-invasive hormonal sexing method.

Material and methods

The feces of three males and three females were collected daily for up to four months (Table 1). Because female "T" has two sampling periods (T1 and T2), seven different symbols are listed in Table 1 (Table 1). All sand in the terrariums was sieved for daily fecal sample collection, and food debris, such as seeds, was removed. The fecal pellets were frozen at -18°C until the extraction started.

In order to allocate the feces individually, the animals were kept in solitary confinement during the sampling period. No fecal samples were collected on a few days, so the sample size in those cases differs from the number of days in the sampling period (Table 1). All elephant shrews were of a suitable age for breeding (Olbricht, 2008; Olbricht & Sliwa, 2010).

Tab. 1: Overview of round-eared elephant shrews and sampling period for this study. The female "T" has two sampling periods (T1 and T2).

symbol	year of birth	sex	keeping conditions	age at the 1st sampling day [months]	sampling period	sample size
A	2014	female	visual and olfactory contact to a male	36	2017-2018	127
T1	2013	female	visual and olfactory contact to a male	39	2016-2017	61
T2	2013	female	no contact to a male	49	2017	118
N	2016	female	no contact to a male	3	2016-2017	61
H	2013	male	visual and olfactory contact to a female	49	2017-2018	124
R	2014	male	visual and olfactory contact to a female	36	2017	12
J	2014	male	no contact to a female	42	2017	9
total sample size						512

For sample extraction, 0.1 g feces were mixed with 2.0 ml methanol and vortexed for 30 minutes. After centrifugation for 15 minutes, the supernatant was diluted at 1:10, and samples were analyzed using established enzyme immunoassays (EIA) for fecal estrogen, progesterone, and androgen metabolites. The antibodies for the EIAs were raised in rabbits (Schwarzenberger et al., 2000). The following immunogens were used to generate the antibodies: 5 α -pregnane-

3β -ol-20-one 3HS:BSA for the 20-oxo pregnane EIA (Schwarzenberger et al., 1996), estradiol- 17β -OH 17-HS:BSA for the estrogen EIA (Patzl et al., 1998) and 5α -androstane-3,17-dione 3-CMO:BSA for the epiandrosterone (=17-oxo-androstanes) EIA (Möstl & Brunner, 1997).

Results

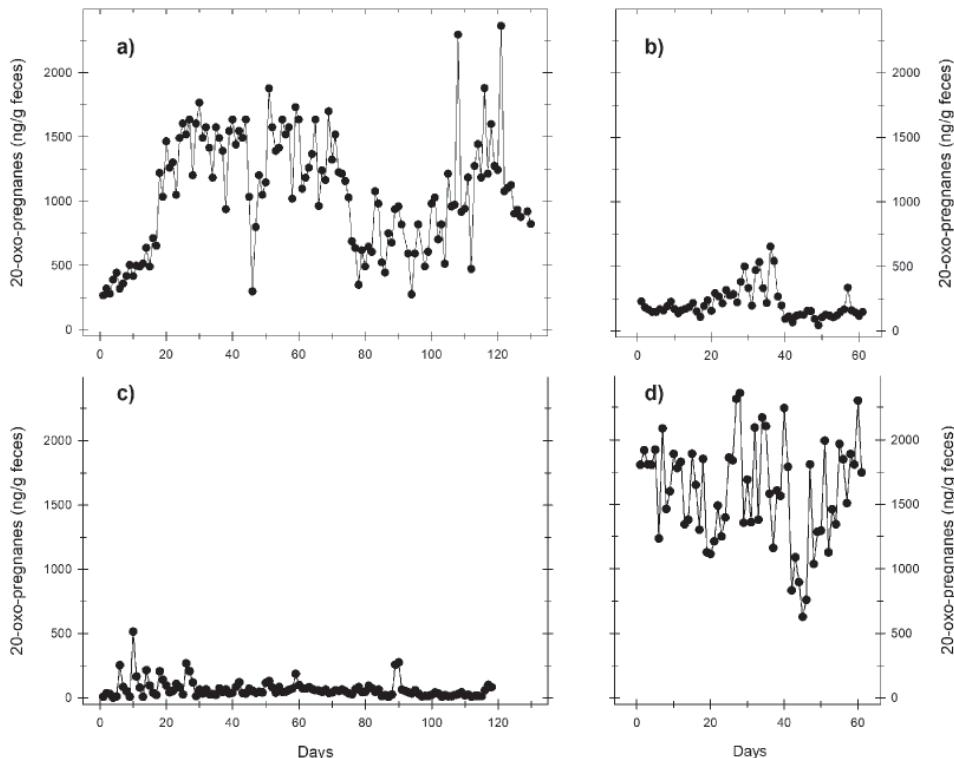


Fig. 1: Fecal 20-oxo-pregnane concentration of female "A" (a), female "N" (b), female "T2" (c) and female "T1" (d). Females "A" and "T1" had visual and olfactory contact to a male whereas Females "N" and "T2" where kept without contact to a male.

The husbandry system influenced the concentration of 20-oxo-pregnanes. Although 20-oxo-pregnanes did not reveal a cyclic pattern, females with visual and olfactory contact with a male had higher concentrations (Fig. 1). In contrast, estrogens were a good indicator of the ovarian cycle, as peak values of these hormones indicated follicular phases (Fig. 2). Females with sight and smell contact with a male had a shorter average cycle length ("A": 8 days; "T1": 14 days) than females without male contact ("T2": 28 days; "N": no cycle detectable) (Figs 1 and 2).

Epiandrosterone concentrations in females varied widely, ranging from 9.3 to 2,400 ng/g feces. The correlation coefficient with 20-oxo-pregnane concentrations was 0.93. In males, epiandrosterone concentrations ranged from 65.7 to 289.4 ng/g feces. However, there was no

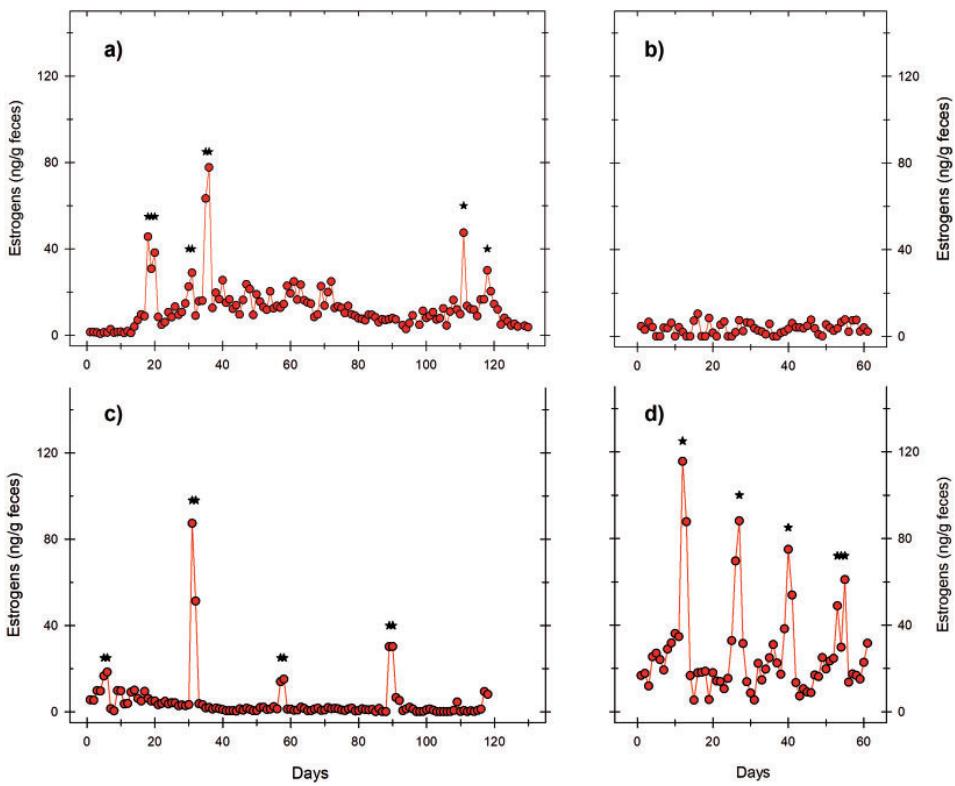


Fig. 2: Fecal estrogen concentration of female “A” (a), female “N” (b), female “T2” (c) and female “T1” (d). Females “A” and “T1” had visual and olfactory contact to a male whereas Females “N” and “T2” were kept without contact to a male. Estrogen values indicating a follicular phase are marked with a *.

significant difference between the epiandrosterone concentration in females and males, and thus it is not possible to identify the sex of the animals by measuring fecal androgen metabolite concentrations.

Discussion

The objective of this study was to obtain data on the female sexual cycle in elephant shrews; for this purpose, methods for non-invasive monitoring of fecal steroid hormone metabolites were established. Female elephant shrews in this study exhibited variable cycle lengths from 6–31 days, with an average cycle length of 15.5 days. The individuals with olfactory and visual contact with males exhibited a significantly shorter cycle and had significantly higher progesterone levels and pronounced estrogen peaks. In contrast, females without male contact exhibited low progestagen concentrations and occasional estrogen peaks. However, in terms of cycle diagnostics, progestagens were not informative. The results of hormone analyses suggest induced

ovulation in elephant shrews. Like in the elephant shrews we studied, higher progesterone concentrations were found in females in opposite-sex groups in species with induced ovulation; for example, in female lions (*Panthera leo*; Schramm et al. 1994) or cheetahs (*Acinonyx jubatus*; Brown et al. 1996). These results suggest that ovulation is triggered by olfactory and visual contact with males (McDermott, 2019; Jorge-Neto et al., 2020). The young female “N” had no contact with a male and showed no ovarian activity during our study, although it could be shown by Olbricht (2008) that other round-eared elephant shrews are reproductively mature in this age and mate successfully for the first time. Our results are supported by similar observations in brush-tailed bettongs (*Bettongia penicillata*; Hinds & Smith, 1992), Pallas’ Cat -(*Otocolobus manul*; Brown et al., 2002) and grey short-tailed opossums (*Monodelphis domestica*; Hinds et al., 1992). However, the small sample size of our study must be considered, and further studies with samples from a higher number of individuals are needed to verify these results.

Breeding elephant shrews in captivity is difficult, and one possible reason is the problem of differentiating sexes and the associated pairing of same-sex individuals (Sicks, personal communication). Therefore, we attempted to develop a noninvasive method for sexing this species using androgen metabolite analysis. However, we were unable to detect significant differences in fecal epiandrosterone metabolite concentrations between female and male elephant shrews, leading us to conclude that this method is unsuitable for sex determination.

Another possible explanation for the difficulty in breeding round-eared elephant shrews is the territorial aggressive behavior of many round-eared elephant shrews in captivity, so the animals must be kept individually. It is possible that females prefer males that are least related to them when choosing mates, as seems to be the case with cheetahs (Kirkpatrick et al., 2006; McDermott, 2019). Due to the high inbreeding rate of elephant shrews in captivity in Europe (Olbricht & Sliwa, 2010), establishing breeding pairs is difficult. However, as no studbook records exist and zoos exchange animals with private keepers, genetic studies would be necessary to determine the degree of inbreeding.

Further studies with larger sample sizes collected from at least eight females are necessary to verify our hypothesis of induced ovulation in round-eared elephant shrews. Because hormonal sexing in round-eared elephant shrews was unsuccessful, a DNA-based methodology using fecal samples should be established in the future.

Acknowledgement

We thank the zoos of Wuppertal, Cottbus, and Berlin (Tierpark) and one private elephant shrew breeder for providing us with animals for fecal sample collection. Feces from other animals were collected from animal keepers at ZOOM Gelsenkirchen. We also thank Elke Leitner for her support in the laboratory work.

Zusammenfassung

Die Zucht von Rüsselspringern ist kompliziert und bislang nur sporadisch erforscht. Daher wurde die tägliche Ausscheidung von fäkalen Östrogen- und Progesteronmetaboliten bei Kurzohrrüsselspringern (*Macrosceles proboscideus*) ($n = 6$) über einen Zeitraum von bis zu vier Monaten mittels Enzymimmunoessay (EIA) analysiert. Die weiblichen Rüsselspringer dieser Studie zeigten eine variable Zykluslänge von sechs bis 31 Tagen und eine durchschnittliche Zykluslänge von 15,5 Tagen. Weibliche Tiere mit Sicht- und Riechkontakt zu einem Männchen

wiesen dabei eine kürzere Zykluslänge (durchschnittlich 11,5 und 13 Tage) sowie eine höhere Progesteronmetabolitenkonzentration im Vergleich zu Weibchen ohne männlichen Kontakt auf. Aufgrund dieser Beobachtung stellen wir die Hypothese auf, dass weibliche Kurzohrrüssel-springer eine induzierte Ovulation haben. Aufgrund fehlender zyklischer Schwankungen der Progesteronkonzentration eignet sich lediglich Östrogen für die nicht-invasive Zyklusdiagnos-tik in Kurzohrrüsselspringern. Angesichts der geringen Stichprobengröße dieser Studie ($n = 6$) ist weitere Forschung notwendig.

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DER ZOOLOGISCHE GARTEN

doi:10.53188/zg0012

Zool. Garten N.F. 91 (2023) 9-39

THE ZOOLOGICAL GARDEN

Large carnivore feeding in European zoos

Die Fütterung großer Carnivoren in europäischen Zoos

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Abstract

While zoo carnivore life expectancy has increased, the question remains how these longer lives are spent. Because feeding management may particularly influence carnivore behaviour, we collected and recorded feeding routines in 44 European zoos in 7 different countries by personal visits. During these visits, we assessed the current feeding situation in zoos, which was achieved by accompanying the responsible staff members on their daily routines with 11 different carnivore species. Meat on bone as a diet item was used by the majority of zoos, and carcass feeding was mainly practiced with small (rodents, rabbit, chicken), but hardly with large carcasses. Whereas many institutions reported a certain repertoire of feeding methods of varying potential enrichment value, during the visits themselves, most institutions used those methods of their feeding repertoire that can be considered less labour-intensive and less enriching. The number of institutions that only used a limited number of feeding methods was unexpectedly high, and methods like swing pole feeders, pulley feeders or self-serving feeders (excl. time-delayed feeders and barrel feeders in bears) were not in use in the visited institutions. Additionally, neither methods that require social carnivores to cooperate to access food, nor other feeding methods during which animals can actually fail to obtain their food (mimicking unsuccessful hunting) were reported. We suggest that in order to more closely mimic natural conditions and possibly enhance carnivore welfare, large carcass feeding in physically and cognitively challenging ways should be used more frequently, with a written feeding management plan to ensure that these feeding methods are not only used sporadically, but at a consistent frequency. Such an approach could at the same time ensure that appropriate resources in terms of facilities, equipment, diet items, and work time are available.

Keywords: carnivores, feeding methods, feeding enrichment, pole feeding, whole carcass, animal fibre

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Introduction

In zoos worldwide, carnivore neonate mortality has decreased, and adult carnivore longevity has increased over the decades (Roller et al., 2021). While this is a positive development, it is nevertheless necessary to monitor how these longer lives are spent by the animals. Carnivore husbandry has been particularly criticised in terms of behavioural deficits (Clubb & Mason, 2003, 2007; Kroshko et al., 2016). While these may not represent threats to survival, they may compromise animal welfare.

Feeding is an important part of zoo animal management. Evidently the dietary regime must provide the animals with the energy and nutrients required for optimal health. This does not only imply an appropriate provision with proteins, fats, minerals, and vitamins, but also with less easily digestible material. In carnivores, these represent, on the one hand, physically challenging components required for dental health, such as the prevention of dental calculus (Bond & Lindburg, 1990; Roe & Cleave, 2005). Studies have also shown that animals fed whole-prey items vs. those fed processed meat suffered fewer gingival health problems, less plaque formation, and less focal palatine erosion (Lindburg, 1988). On the other hand, less digestible material represents substrates summarised as ‘animal fibre’, i.e., bones, tendons, cartilage, skin, hair, and feathers including collagens, glycosaminoglycans and keratin (Depauw et al., 2012, 2013). These substrates have fermentation properties that lead to specific conditions in the hindgut; in particular, they may temper the negative side effects of protein fermentation into putrefactive compounds (Depauw et al., 2012, 2013). Whole prey is considered to provide an appropriate and balanced proportion of ‘animal fibre’ in comparison to pure meat, because of these less fermentable substances (Depauw et al., 2012, 2013). Free-ranging carnivores use variable feeding strategies (De Cuyper et al., 2018); carnivores hunting comparatively small prey typically ingest the whole prey animal, whereas carnivores that hunt large prey may – especially during periods of plentiful prey presence – decide to only ingest the more digestible parts. Therefore, actual ‘animal fibre’ intake in natural habitats may be particularly variable for large-prey predators.

Furthermore, feeding has important consequences for behaviour. The ease with which animals can ingest their food, and the ease with which they can obtain it, defines the occupational value provided by that food. For example, a portion of minced meat will require less time of appetitive foraging behaviour than a similar amount of whole meat that requires more complex oral processing. Similar differences will occur when feeding whole meat with and without bone, or pieces of a carcass with or without skin and fur, or whole carcasses with or without the digestive tract. Veninga & Lemon (2001) found that a pack of African wild dogs (*Lycaon pictus*) required a much longer feeding time for a whole carcass (60 minutes) as compared to a similar amount of pieced meat (3 minutes). For cheetahs (*Acinonyx jubatus*), Bond & Lindburg (1990) reported improved appetites, longer feeding bouts, and a greater possessiveness of food in animals that were carcass-fed. For social carnivores, large carcass feeding has been suggested to have positive effects on social cohesion (Macdonald, 1996; Höttges et al., 2019). Therefore, the use of whole prey feeding has been advocated from a behavioural point of view. Table 1 gives an overview of typical diet items used in carnivore feeding.

Similarly, different ways exist that make obtaining food a more complex procedure. Evidently, a lump of minced meat put in front of the animal requires less time for ingestion than the same quantity of minced meat distributed across various locations within the enclosure. Spreading the provided food over different locations, either by hiding, scatter feeding, or by making small quantities available from feeders at regular or irregular intervals, is a simple way of increasing the occupational value of the food (Table 2). This is particularly appropriate for animals consuming small prey, but less feasible for animals feeding on larger prey. For animals of the latter group, a variety of methods have been proposed to make access to diet items more

Tab. 1: Typical diet items used in feeding of zoo carnivores, their reported use in the 44 European zoos that participated in the present study, and the percentage of those zoos that reported their use in which these diet items were personally observed during the survey visit.

Item	Description	Reported in zoos	of which personally observed
Minced / Processed meat	Meat and similar products, made into a relatively homogenous mass that has a dough-like consistency and little physical structure, often supplemented with essential nutrients – mainly commercially available products, which may come as raw meat, heat-processed moist (mainly canned) food, or dry (mainly extrudates)	2%	0%
Commercial preparations	Commercially available food, such as dog/cat/zoo carnivore dry and wet foods and pellets (especially for bears)	30%	38%
Organs	Any kind of organ whole or chopped up	45%	20%
Whole meat	Cuts of meat in various sizes (from golf ball size to several kilograms) – mainly from large (prey*) animals	55%	42%
Meat on bone	Meat pieces still connected to the bone – mainly from large (prey*) animals	98%	72%
Whole meat with fur/feathers	Cuts of meat with skin and fur but without bones – mainly from large (prey*) animals	23%	10%
Carcass parts with fur/feathers	Carcass parts with meat attached to bone, skin and fur (e.g., ¼ deer carcass cut up) – mainly from large (prey*) animals	57%	12%
½ carcass	½ carcass with skin and fur intact and organs still inside the carcass – mainly from large (prey*) animals	30%	15%
Complete eviscerated carcass	Carcass without any organs – large or small prey*	0%	0%
Carcass without digestive tract	Carcass without intestines, but still with red organs – large or small prey*	30%	15%
Decapitated carcass	Carcass without head – large or small prey*	20%	22%
Whole carcass	Complete carcass unopened or with abdomen opened – large or small prey*	95%	38%

*‘prey’ includes domestic animals; large prey examples are cattle, sheep, goats, deer, horses, donkeys, or zoo hoof stock; small prey examples are rodents, rabbits, juvenile or adult poultry, or zoo rodents

challenging, some of which can also be used to make access to a single small diet item more challenging for small-prey feeders (Table 3).

Tab. 2: Feeding options used in feeding of zoo carnivores, their reported use in the 44 European zoos that participated in the present study, and the percentage of those zoos that reported their use in which these feeding options were personally observed during the survey visit.

Option	Description	Example references	Reported in zoos	of which personally observed
One portion (per animal)	One pile of food in the enclosure easily accessible for the animal		100%	80%
Group feeding	Animals are fed in a group with whole carcass to share among them		NA	NA
Scattering	Pieces of the offered food scattered around the enclosure	(Law et al., 1997; Andrews & Ha, 2014)	68%	47%
Hiding	Hiding the food within the enclosure	(Fischbacher & Schmid, 1999)	64%	68%
Time-delayed dispensing	The food is distributed or dispensed at various (non-random or random) times during the day	(Shepherdson et al., 1989; Carlstead et al., 1991; Fischbacher & Schmid, 1999)	9%	25%

NA not assessed in the present study

Hand feeding means the animals receive their meals in mouth-sized pieces by a long tweezer directly into their mouth. If food is provided loose on the ground, the food will either be thrown in, placed on the ground of the enclosure, or in a food dish. The meals can also be tied to the ground with the help of a carabiner in stones, logs, or other objects within the enclosure. The animal must pull the meat off to access its meal or eat at the fixed spot.

Hanging up food on ropes or carabiners in different heights is a widely used method in any carnivore (Fig. 1A) and can be combined with any enclosure structure so that the animal has to first climb to the spot where the food is hung. To make it more challenging, a weight can be attached to the other side of the rope so if the food is let go, it will be pulled back up and the individual must begin from the start; alternatively, similar constructions can facilitate that another animal, a keeper or visitors pull at the other side of the rope (Fig. 1B). O'Neal (2011) describes the use of carcass hanging on an elastic cord in Tasmanian devils (*Sarcophilus harrisii*), where the carcass is secured to a bungee cord that is attached in the devils' enclosure and left dangling above the ground. This should increase the effort for food acquisition, and promotes behaviours strengthening muscles necessary for social feeding and carcass tearing. A swing-pole feeder is a container with a hole cut in the base which can be fixed to the roof inside the enclosure. A free-swinging branch attached to the underside of the roof provides access to the container. The cats climb onto the branch and thrust their paws through the opening to reach the food (Law et al., 1997). Feeding sticks involve wooden stick-like objects which can be fitted with simple wooden spigots at one end and hooks at the other. The stick can be repositioned for each feed so that the cat does not have easy access to it by means of an adjacent branch but must put some effort into obtaining the food. Cats will leap from the floor and cling to the stick, supporting their body weight, while fighting to free the food from the wooden spigot (Law et al., 1997). On other occasions, the food may be procured by jumping from the nearest log onto the stick after exploring which launch point is nearest to the stick (Law et al., 1997).

The feeding pole consists of a wooden pole or tree (Fig. 1D), which can vary in height, with e.g. a loose-fitting wooden spigot hammered into the top (Law et al., 1997). The food item, such as part of a horse or cow leg, is hung on the peg. The original publication suggests that only one animal should have access to the pole at a time to avoid rivalry, but since its appearance, several zoological institutions have successfully been using several poles for the corresponding

Tab. 3: Methods used in feeding of zoo carnivores, their reported use in the 44 European zoos that participated in the present study, and the percentage of those zoos that reported their use in which these feeding methods were personally observed during the survey visit.

Method	Description	References	Reported in zoos	of which personally observed
Hand feeding	Food is provided with long tweezers directly into the mouth of the individual	(O'Neal, 2011)	11%	80%
Loose on the ground	Food is either thrown in, placed on the ground of the enclosure or in a food dish	(Hare & Jones, 2018)	100%	93%
Tied to the ground	Food is tied to objects such as trees, rocks on the ground level	(Law et al., 1997)	59%	35%
Hung up	Food is hung up on any available place in the enclosure	(Law et al., 1997)	84%	46%
Hung up with counterweight	Food is hung up with a weight on the opposite site of a rope, which pulls the food back up as soon as released	(Law et al., 1997)	2%	0%
Hung up with option of being pulled at the opposite site	Food is hung up with the option of being pulled against at the opposite	(Law et al., 1997)	2%	0
Hung up elastic cord	Food attached to elastic cord dangling over ground	(Law et al., 1997)	25%	99%
Swinging platform	Moving platform off ground under hanging food	(Law et al., 1997)	5%	50%
Woodpile feeder	Food under branches piled together	(Law et al., 1997)	2%	100%
Feeding stick	Food stuck to a stick hung from some high point; animal must cling to stick while getting food off	(Law et al., 1997)	2%	0%
Swing pole feeder	Box with a hole at the base bolted to the roof, access via a swinging pole underneath it to which the animal must cling	(Law et al., 1997)	0%	0%
Self-serving feeder	Individuals can get food by themselves from certain objects in their enclosure	(Law et al., 1997; Gusset et al., 2002; Andrews & Ha, 2014)	0%	0%
Movement induced	Object with holes, comes in all different shapes, and sizes which releases food when moved around	(Law & Kitchener, 2002; Law & Reid, 2010; Hare & Jones, 2018)	16%	0%
Pole feeding	Wooden pole with food at the top	(Quirke et al., 2013; Fischer et al., 2021)	20%	44%
Run	Lure system to stimulate the hunting instinct	(Quirke et al., 2013; Fischer et al., 2021)	5%	0%
Zipline feeding	Zipline within the enclosure incl. a device to connect food, can move forwards and backwards along the line	(Quirke et al., 2021)	18%	50%
Pulley feeder	Zipline connected with fire hose, food attached to a track runner out of reach	(Hare & Jones, 2018)	0%	0%
Novel objects / self-built	Novel objects either self-built or commercially purchased		16%	57%
Dug in ground	Food dug into the ground at different depths		16%	14%
Swimming	Food presented in different locations, for the animals only to be reached while swimming		23%	20%

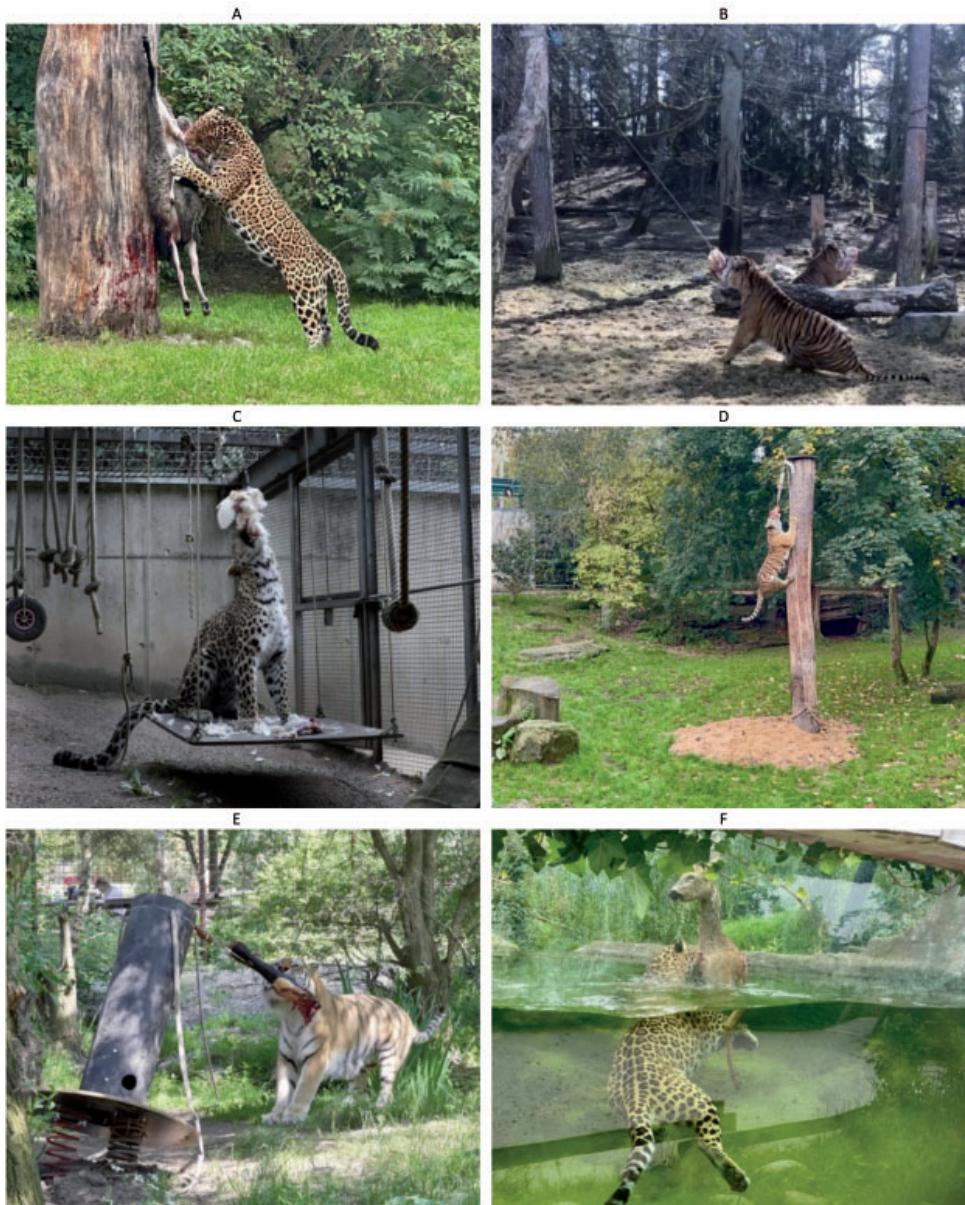


Fig. 1: Examples of different feeding methods for large carnivores: (A) carcass tied to a tree, Parken Zoo, Sweden; (B) counter-pulling system for two animals, Parken Zoo, Sweden; (C) swinging platform – Cologne Zoo, Germany; (D) pole feeding, Cologne Zoo, Germany; (E) self-built feeding object, Odense Zoo, Denmark; (F) food presented over water, Randers Regenskoven, Denmark. 1C copyright by Dr. A. Sliwa, Cologne Zoo; all other photos: Cellina Kleinlugtenbelt/ Anita Burkevica.

number of animals simultaneously. The carnivore climbs the pole, grabs the food, and climbs or jumps back down (Law et al., 1997). Felids use the same muscles when climbing trees as they do when grappling with and pulling down a large prey animal, such as a wild water buffalo (*Bubalus arnee*) or sambar deer (*Rusa unicolor*) (Turner & Anton, 2000). Therefore, climbing a pole to access food provides a realistic simulation of the physical activity required by big cats when they hunt (Law & Kitchener, 2019).

Swinging food platforms are suspended off the ground by a wire cable at each of the corners. The meat is attached to a rope or bungee cord directly above the platform, so the individual has to stand up on the moving platform, balancing while trying to remove the meat from the cord (Hare & Jones, 2018) (Fig. 1C).

A specialised coursing system often called the ‘cheetah run’ has been adopted at various institutions worldwide to simulate the cheetah’s hunting and serve as an enriching activity, which can also be used for other species (Fischer et al., 2021). Animals are trained to chase the lure and sometimes receive a reward after the completion (Quirke et al., 2013; EAZA, 2018). A different variant of the lure chasing system is a food chasing system which works the same way but instead of getting a reward after the completion, the individuals chase after their meal portion which will be received at the successful ‘hunt’. Some may use a similar system to the one used for coursing greyhounds, which consists of a car starter motor operated by a hand held trigger switch, a string with a lure, is powered by a car battery, and pulleys are used in order to set out the course of the lure (Quirke et al., 2013).

Ziplines can be easily constructed by a metal rope attached on both ends inside the enclosure; with a carabiner or a roll construction, food can be attached to the zipline and will move back and forth if the animal is trying to pull it off. The pulley feeder is a zip line design to promote cooperative physical exercise for animals that hunt in a group, e.g., African hunting dogs (Hare & Jones, 2018). Ideally set on a hillside enclosure the food item is attached to a track runner and when resting at the bottom of the slope it is out of reach for the pack. A strip of fire hose or rope dangling from the runner must be used to drag the meat back up the hill, pull it down, and hold it in place while others feed (Hare & Jones, 2018) (Fig. 2A). Similar setups, which have apparently not been used widely for other purposes than research, allow access to food only when at least two animals cooperate, e.g. when pulling at the same time at different ropes (Drea & Carter, 2009; Marshall-Pescini et al., 2017; Borrego, 2020) (Fig. 2B-D).

Woodpile feeders are branches piled together which provide a complex lattice in which food can be hidden. These feeders increase the effort and time spent searching for food (Law et al., 1997).

Furthermore, electronic feeders can be used in all carnivores. A sufficient quantity of food is distributed to the feeding box, which is closed by a sliding door with a strong magnet (Jenny & Schmid, 2002). When the magnet is turned on the animal cannot open the door. Each magnet can be switched off during certain periods of time, randomly spread over the day, which happens without any associated noise (Jenny & Schmid, 2002). Electronic feeders are available in all different shapes and sizes, such as electronic scatter feeders which are placed above the ground and scatter certain foods, e.g. pellets for bears randomly throughout the day (Andrews & Ha, 2014). Self-serving feeders are available in various options. The main concept is that the individuals can feed whenever they want from a certain quantity of food placed in the self-serving feeder, which will fill up whenever emptied. This mechanism permits a continuous supply of e.g. pellets for bears but prevents them from spilling or playing with the food (Ziegelmüller & Nolte, 1997).

Movement-induced dispensers range from balls to barrels; basically, holes can be put into anything. They all work with the same principle: food will fall out as soon as the object containing it is moved around. The dispensers can either be left on the ground or hung up. Different



Fig. 2: Examples of different feeding methods to display or test cooperative behaviour in large carnivores: (A) pulley feeder for cooperative canids, as described for African hunting dogs (by Hare & Jones (2018); screenshot from an uncredited video no longer available on YouTube); (B) cooperation task in spotted hyenas; photograph from Drea & Carter (2009); (C) cooperation task in wolves; photograph from Marshall-Pescini et al. (2017); (D) cooperation task in lions; photograph from Borrego (2020).

constructions such as the ‘wobble tree’ are also available for the use in bears, where food is placed in a container on top of a long flexible pole, which is too thick for breaking and too smooth for climbing; to obtain the food the bear must shake it (Law & Kitchener, 2002).

However, the methods mentioned above are not the only ones existing. Motivated, committed people can create their own methods, with few limits set to the imagination on how to feed carnivores in a more challenging way. The overall objective of the present study was to collect

data on frequently used feeding methods and used food items for large carnivores in a variety of European zoos. The ultimate goal of this paper is to provide animal care professionals in zoos a potential framework to explore, evaluate and also get new ideas on how to feed captive large carnivores.

Materials and methods

This study was supported by the EAZA Felid TAG and Canid and Hyeanid TAG. We collected and compiled data from 44 zoos in 7 countries by personal visits; one zoo sent their information in since a personal visit was not possible due to COVID-19 restrictions. Thus, we observed 69 tigers (*Panthera tigris*) (26 zoos), 119 lions (*Panthera leo*) (31 zoos), 16 jaguars (*Panthera onca*) (7 zoos), 28 leopards (*Panthera pardus*) (15 zoos), 27 snow leopards (*Panthera uncia*) (13 zoos), 55 cheetahs (*Acinonyx jubatus*) (15 zoos), 40 lynxes (*Lynx lynx*) (16 zoos), 27 hyenas (*Crocuta crocuta* and *Hyaena hyaena*) (11 zoos), 75 wolves (*Canis lupus*) (16 zoos), 66 brown bears (*Ursus arctos*, including one brown bear – polar bear hybrid) (15 zoos), and 36 polar bears (*Ursus maritimus*) (12 zoos) during their feeding to find out what feeding methods are used, how they are applied and how the animals react to them. This was done by following the responsible staff members on their daily routines with the selected species, both from behind the scenes and from the point of view of a visitor. During personal interviews with the responsible staff members, we gained more information about used feeding options, whether the animals interact with them, and how they are approached. The interview was based on a pre-planned set of questions but was conducted as a free-flowing conversation rather than a structured ticking off from the individual questions. All interviews were conducted by the first author. Feeding was documented with photos and videos. The interview included details about the used diet items, feeding options and frequently used methods. We divided the results into two types: what was stated during the interviews, and what was observed during the actual feeding during the visit. Some feedings could not be observed in person due to the presence of offspring, the separation of diseased individuals, the current hygienic rules at a zoo due to the current COVID-19 outbreak, and current hibernation of several bears.

The diet items, feeding types and feeding methods were defined as in Tables 1-3.

Results

The information obtained and the observations made during the visits are given on a species basis in Tables A1-A11 in the appendix. Here, we report on the major findings.

Diet items (Table 1)

Meat on bone was used by the majority of zoos for most of the species with a percentage of 98% closely followed by whole carcass with 95%. With a lesser frequency, the use of carcass parts with fur or feathers (57%), whole meat (55%) and organs (45%) was reported. At a lower frequency, 30% of zoos used commercial preparations as part of their diet plan, $\frac{1}{2}$ carcass or carcass without the digestive tract. 23% used whole meat with fur or feathers and 20% decapitated their whole carcasses before feeding them to their carnivores. Minced and processed meat with 2% and complete, eviscerated carcasses with 0% were used the least in all species.

Whole carcass use was reported in 94% of lynxes, 91% of hyenas, 87% of leopards, 85% of tigers, 84% of lions, 81% of wolves, 77% of snow leopards, 73% of cheetahs, 71% of jaguars, 50% of polar bears and 47% of brown bears. It was less frequently personally observed during the visit - in 5 out of 15 zoos that stated the use for their lynxes, 3/10 for hyenas, 6/13 for leopards, 3/22 for tigers, 2/26 for lions, 2/13 for wolves 4/10 for snow leopards, 4/11 for cheetahs, and 2/5 for jaguars. In none of the zoos were bears fed whole carcass during our visits due to the reduced feeding in the autumn and winter periods.

When splitting the reported use of carcasses by the size of the carcass (large carcass: considered everything as big as a goat or bigger, incl. juvenile goats/sheep older than 4 months; small carcass: everything up to the size of a goat, incl. juvenile goat/sheep up to 4 months), a distinct difference was evident (Fig. 3, Table 4). Large carcasses were used very rarely by the visited zoos; only 2 zoos used large carcasses on a weekly basis. The majority of zoos did not use large carcasses at all, or only very sporadically (Fig. 3A). By contrast, small carcasses were frequently used, with a majority of zoos using them at least once per week (Fig. 3B).

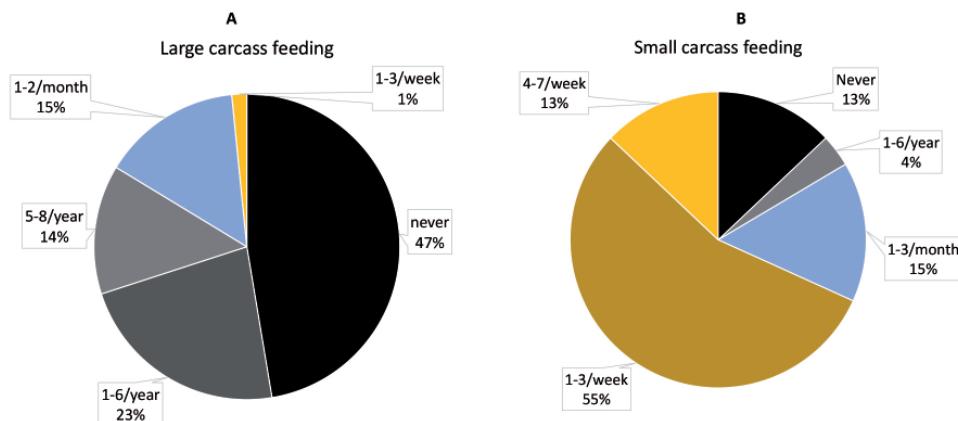


Fig. 3: Summary of the use of (A) large and (B) small carcass feeding for 11 species of large carnivores in 44 European zoos.

Although not quantified in the present study, interviews often suggested that the responsibility for choosing a diet item can differ: it may lie with the zoo commissary or a person higher up the zoo hierarchy than the keepers, and more rarely with the keepers themselves.

Feeding option (Table 2)

The option of feeding each animal one portion was used the most with 100% of all visited zoos reporting it. Unfortunately, group feeding was not systematically included in the questionnaire, but it can be expected that wherever large whole carcasses are fed, it most likely is for a group to share. This method was observed in two zoos. Scattering the food was reported by 68% of zoos with the majority using this option for brown bears (67%), 64% used the option of hiding the food within the enclosure, e.g., in novel objects and 9% indicated the use of time-delayed dispensing at various random and non-random times during the day. The latter method was reported the most in polar bears with 17%, none of the zoos (0%) used this method in cheetahs, lynxes, hyenas and wolves.

During the personal visits, one portion-feeding was observed in 80%, hiding in 68% and scattering and time-delayed dispensing in 47% and 25% of the zoos reporting the respective use.

Tab.4: Overview of the frequency of large and small carcass use in feeding of zoo carnivores, their reported use in the 44 European zoos that participated in the present study, and the percentage of those zoos that reported their use.

	Tiger	Lion	Jaguar	Leopard	Snow leopard	Cheetah	Lynx	Hyena	Wolf	Brown bear	Polar bear
<i>Large carcass feeding</i>											
never	9 (35%)	7 (23%)	5 (71%)	9 (60%)	6 (46%)	11 (73%)	13 (81%)	8 (73%)	2 (13%)	10 (67%)	10 (83%)
1-6/year	4 (15%)	6 (19%)	1 (14%)	3 (20%)	4 (31%)	1 (7%)	1 (6%)	-	2 (13%)	1 (7%)	2 (17%)
5-8/year	5 (19%)	7 (23%)	1 (14%)	-	2 (15%)	2 (13%)	1 (6%)	1 (9%)	4 (25%)	3 (20%)	-
1-2/month	7 (27%)	10 (32%)	-	2 (13%)	1 (8%)	1 (7%)	1 (6%)	2 (18%)	3 (19%)	1 (7%)	-
1-3/week	-	1 (3%)	-	-	-	-	-	-	1 (6%)	-	-
<i>Small carcass feeding</i>											
never	1 (4%)	2 (6%)	-	-	1 (7%)	1 (7%)	1 (6%)	2 (18%)	3 (19%)	8 (53%)	6 (50%)
1-6/year	1 (4%)	6 (23%)	7 (23%)	3 (43%)	1 (7%)	2 (15%)	1 (7%)	-	-	1 (7%)	-
1-3/month	6 (23%)	20 (62%)	4 (57%)	9 (60%)	6 (46%)	9 (60%)	11 (69%)	8 (73%)	2 (13%)	-	3 (25%)
1-3/week	14 (54%)	2 (8%)	-	4 (27%)	4 (31%)	4 (27%)	3 (19%)	-	5 (33%)	2 (17%)	2 (17%)
4-7/week	-	-	-	-	-	-	-	-	2 (13%)	1 (7%)	-

In many cases, keepers mentioned that it was their own responsibility to choose a feeding option. In the case of mechanical dispensers, it was stated repeatedly that the use of these machines was dependent on their maintenance and state of functioning. No written instructions on the use or frequency of feeding options were indicated.

Feeding method (Table 3)

All of the zoos reported placing food loose on the ground (including platforms), e.g., in a pile, which was practiced in 100% of leopards, snow leopards, cheetahs, hyenas, and polar bears but only in 60% of brown bears. 84% of zoos reported hanging up food; this was used only in 20% of brown bears but 86% of jaguars. 59% reported tying the meal to the ground with a majority using this method in their tigers (69%), 25% hung it up attached to a bungee cord, 20% used a pole feeding method of which 15% used it for tigers and 43% for jaguars. 18% indicated the use of a zipline construction, 16% a movement-induced dispenser, 11% handfed their carnivores, 5% used a run and another 5 % a swinging platform. The swinging platform was only used in leopards. 2% hung up the food with a counterweight or used a woodpile feeder or a feeding stick, and no facility used a swing pole feeder, self-serving feeder, or pulley feeder.

Observations on the day of visit were: loose on the ground – 93%, hand feedings – 80%, swinging platforms and ziplines – 50%, hanging up the meal – 46%, pole feedings – 44%, tied to the ground – 35%, hanging on an elastic cord – 9%, counterweight hanging up, feeding sticks, movement induced dispensers and run constructions – 0%.

In addition to the methods listed in Table 3, various self-built options and novel objects were in use. 16% of the zoos built several options themselves (e.g., Fig. 1E), of which a third were zoos with tigers and a quarter with polar bears. These methods were observed in 57% of the zoos that reported their use. 16% of zoos reported hiding the food being dug into the ground for the animals to find,

mainly in hyenas (36% of institutions keeping hyenas). This was actually observed in 14% of institutions reporting this method. 23% reported presenting the food on or in water, mainly for polar bears (30%). This was observed in 20% of the zoos reporting this use. One zoo practiced hanging a carcass over water for jaguars who had to detach the carcass while swimming (Fig. 1D). Across all species, half of the zoos either used only feeding loose on the ground and hand feeding or an additional method (Table 5).

Subjectively, the speed of consuming the meal was faster when feeding by hand or placing the food loose on the ground without any obstacle compared to any other discussed feeding method, such as pole feeding and bungee cord feeding.

Although not quantified in the present study, interviews mainly did not point out a person responsible for the choice or the frequency of use of feeding methods. No written instructions on the use or frequency of feeding methods were indicated; however, in individual cases, an unwritten, clear concept of this frequency was evident during the interviews.

Tab. 5: Number of additional feeding methods excluding hand feeding and placing food loosely on the ground.

Species	Zoos using additional methods to feeding loose on the ground and hand feeding							
	0	1	2	3	4	5	6	7
Tiger	1 (4%)	3 (12%)	4 (15%)	8 (31%)	6 (23%)	1 (4%)	3 (12%)	0 (0%)
Lion	6 (19%)	7 (23%)	6 (19%)	5 (16%)	5 (16%)	1 (3%)	1 (3%)	0 (0%)
Jaguar	0 (0%)	2 (29%)	1 (14%)	2 (29%)	1 (14%)	1 (14%)	0 (0%)	0 (0%)
Leopard	3 (20%)	3 (20%)	5 (33%)	3 (20%)	0 (0%)	1 (7%)	0 (0%)	0 (0%)
Snow Leopard	3 (23%)	3 (23%)	4 (31%)	2 (15%)	1 (8%)	0 (0%)	0 (0%)	0 (0%)
Cheetah	8 (53%)	5 (33%)	0 (0%)	2 (13%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)
Lynx	5 (31%)	5 (31%)	2 (13%)	2 (13%)	0 (0%)	0 (0%)	2 (13%)	0 (0%)
Hyena	5 (45%)	1 (9%)	4 (36%)	1 (9%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)
Wolf	10 (63%)	2 (13%)	1 (6%)	2 (13%)	1 (6%)	0 (0%)	0 (0%)	0 (0%)
Brown bear	3 (20%)	4 (27%)	2 (13%)	2 (13%)	2 (13%)	0 (0%)	1 (7%)	1 (7%)
Polar bear	4 (33%)	3 (25%)	2 (17%)	2 (17%)	0 (0%)	0 (0%)	1 (8%)	0 (0%)
average (%)	28%	22%	18%	17%	7%	3%	4%	1%

Discussion

In this study we recorded, the current situation of large carnivore feeding methods in European zoos for different large carnivore species managed at 44 zoological institutions to record the status quo on the variety and frequency of food items and feeding methods in use. The information obtained indicates that the visited zoological institutions use a variety of diet items and methods.

Carnivores in the wild are able to perform appetitive foraging behaviours – looking for prey, stalking, capturing, killing and processing. These behaviours are typically not successful each time they are executed; for example, van Orsdol (1984) reported hunting success of lions in Uganda varying between 27% and 34%. In contrast, these behaviours have been described as permanently not occurring in managed environments like zoos (with the possible exception of processing in the case of whole carcass feeding); the ensuing frustration and behaviour regulation dysfunction has been suggested to contribute to stereotypies (Jenny & Schmid, 2002). The option of using live prey to make offer a surrogate hunting experience to zoo carnivores, though possibly even accepted by a majority of zoo visitors (Ings et al., 1997; Lemmen et al., 2008), is not considered ethically acceptable in many instances because while increasing the welfare of animals (here: predators) is a clear aim, this should not be achieved by compromising the welfare of other animals (here: prey).

Therefore, other options are required to make feeding an important behavioural part of the day. To have animals work for their food in a cognitive challenging but also biologically appropriate way can provide animals with an opportunity for learning and remembering relevant skills that help them control their ability to access and procure food (Meehan & Mench, 2007). Complex, challenging feeding methods can be seen, proactively, as a way to offer positive welfare; alternatively, they can be seen, reactively, as a preventative or curative measure against behavioural indicators of negative welfare (Wagman et al., 2018). The viewpoint – proactive or reactive – may depend on the individual facility's self-understanding as an institution dedicated to creating naturalistic husbandry environments, or as an institution operating under historical burdens that affect husbandry.

In the present study, several observations stood out: (i) The low frequency of large carcass feeding; (ii) that during the visits themselves, mostly those methods of the facilities' repertoires were used that can be considered less labour-intensive and less enriching; (iii) the large number of institutions that only used a very limited number of feeding methods; and that none of the visited zoos used written protocols that defined the frequency of use for the different feeding methods.

Limitations of this study

Several limitations of the present study need to be mentioned. With 44 the number of zoological institutions was low compared to the overall number of EAZA zoos existing in Europe. Theoretically, a larger number of institutions could have been included by using a questionnaire approach, but our focus was on personal visits that, in the experience of the senior author, often better reflect husbandry reality, and may also lead to insights that cannot be gleaned from survey answers. The COVID pandemic limited the visit options in the time window available for the study.

The potentially most important limitation was the time available for the zoo personnel during the visit. Given that the interview, including the visit of the institutions, introduction to the animals and the preparation of the food most likely represented an additional time expense on the part of the zookeepers, it may be understandable that in order to compensate, the more labour-intensive feeding methods were not used during the visit. Alternatively, one might have expected that the visits – which were announced well in advance and coordinated with the zoological institution to accommodate to the disposability of the carnivore staff – might have been an incentive to show off the more elaborate feeding methods available. Either way, it remains difficult to interpret the observation that in the majority of cases, the more labour-intensive feeding methods were not used. Nevertheless, this finding emphasises that on average, these methods have not become part of the invariable routine in the participating zoos but are still being used on a more selective basis. Yet, some zoos include these methods in their daily routines to the extent that the reported more complicated feeding options were actually used, also on the day of visit.

A topic that was left out deliberately in the present study was the question who is responsible for choosing diets, what feeding methods are available at the institution, and the actual use of feeding methods. We expected little gain in results that ascribe this responsibility to certain members of the zoo team (like 'the keepers', 'the curators', 'the commissary personnel', 'the veterinarians'), and suspected that this would vary between institutions. We had the impression of a trend that the diet items used were decided by groups different from the keepers, and that the daily use of a feeding method was more within the scope of keepers' decisions. However, in the case of intended adjustments to a current dietary regime, all groups would have to work cooperatively to define a new goal and put it into practice.

Diet items: large carcass feeding

The historical approach to carnivore feeding was the provision of meat, which needs to be supplemented to avoid evident deficiencies such as calcium deficiency (Allen et al., 1996). Actually, minced meat products, fully supplemented, are used for large carnivore feeding in zoos (Allen et al., 1996; Young, 1997), but these feeds appear to be less popular among European zoos, including the ones of the present study. The necessity of supplementing such a diet with bones for dental health is well known, as is the lack of stimulus they provide for the cranial muscles (Young, 1997). As an evident alternative to adding supplements and structural components to a (minced) meat diet, whole prey feeding has been promoted as well, since it is considered to provide an appropriate and balanced proportion of ‘animal fibre’ in comparison to pure meat, because of less fermentable substances, such as bones, tendons, cartilage, skin, hair, and feathers (Depauw et al., 2012, 2013).

Research on the effects of whole-prey feeding is still limited, but the general current impression is that it is considered beneficial in physiological and behavioural terms (Bond & Lindburg, 1990; McPhee, 2002; Cloutier & Packard, 2014). For example, Wood & Norris (2000) underlined the importance of recognising that physical forms of foods greatly influence the feeding behaviour of captive carnivores. This psychological benefit of a natural diet cannot be imitated or even duplicated with a processed diet form (Roe & Cleave, 2005). Whole prey closely resembles the natural diet of carnivores, even if differences in the body composition of wild prey and domestic animals – which typically represent the source for whole prey – are well-documented (Veninga & Lemon, 2001; McPhee, 2002; Gaengler & Clum, 2015). The documentation of such differences should not lead to the conclusion that they are so large as to make domestic animals an unsuitable food for zoo carnivores; anyhow, the main other options of carnivore feeding are also based on domestic animal products.

Whole prey feeding might be a valuable contribution to a nature-oriented carnivore husbandry. The structure, texture and palatability of whole carcass feeding does encourage various natural behaviours and therefore helps avoiding monotony (Roe & Cleave, 2005). One aspect of large carcass feeding that should be further investigated is its effect on group behaviour. Large carcass feeding may lead to agonistic interactions between group members all feeding on the large carcass, and fear of such conflicts may be one reason why some zoo managers do not want to include it in the feeding regime. However, assuming that social tensions will require an outlet, Höttges et al. (2019) suggested that a large carcass provides such an outlet in a specific situation. Resolving social tensions in a feeding context may lead to less conflict at other times where no additional motivation (feeding) might temper the encounter. In anthropocentric terms, large carcass feeding might offer a comparatively safe stage for solving social conflicts.

Given the relevance of large carcasses for large carnivores, one might assume that anyone – from visitors to animal managers – knowledgeable about the natural feeding behaviour of large carnivores would intuitively understand the value of large, whole carcass feeding. Nevertheless, large carcasses were used very rarely in the zoos that participated in the present study. We could not quantify reasons for this remarkable finding. On the one hand, these may lie in the additional logistic effort required to acquire large carcasses (Allen et al., 1996) and to clean enclosures after large carcass feeding (Young, 1997). Additionally, these may be related to the fact that in many institutions, husbandry routines require a daily or even more frequent shifting of the animals between enclosures, which is traditionally being done by feeding certain (smaller) portions of food. On the other hand, they may lie in a real or assumed unease of zoo visitors with large carcass feeding. It is difficult to judge how justified this perception is. Actually, several studies performed in different countries showed that zoo visitors are not generally opposed to carcass feeding, and actually perceive it as valuable for the animals and believe that there is also an

educational value in feeding whole carcass (Veninga & Lemon, 2001; Gaengler & Clum, 2015; Roth et al., 2017 incl. several unpublished studies). In some human societies, there probably is a cognitive dissociation, or the lack of an association, between the practice to consume meat and the killing of animals that is a prerogative for that practice. While there may be reasons to cherish an absence of a conscious condoning of killing in terms of our human civilisation, this dissociation appears difficult to reconcile with the mission of nature education and concepts of sustainability, which are based on an accountability for our actions. Given its combined effect of nutritional value, behavioural management, and public education, the general lack of large carcass feeding is one of the surprising findings of the present study. Large carcass feeding represents a physical challenge for commissary personnel and keepers, and may not blend easily in the management systems of some institutions that depend on frequent shifting of animals currently accomplished by small portion feeding. Therefore, decisions to promote this feeding need to be flanked by measures that make large carcass feeding logically feasible, possibly requiring – depending on the institution – different degrees of constructional, equipment, and animal management and training measures.

Finally, large carcass feeding is most likely linked to an alternating feeding and fasting regime (Kleinlugtenbelt et al., subm). Apart from representing the natural biology of the species and the corresponding behavioural, physiological and educational effects, variation between individual days might to a certain degree enhance visitor frequency or enhance motivation for visitors to acquire subscriptions, given that there may be an incentive to observe the other day's condition.

Large carnivore feeding methods

The easiest, least time-consuming method (simply placing the meal inside the enclosure on the ground or throwing the portions over the fence) was the most used one during the visits to the zoological institutions. As a slight modification of this method, tying the food to the ground, or hanging it from some enclosure structure, was widely used (Table 3, Tables A1-11). While arguably being cognitively more stimulating than food put loosely on the ground, most of the observations indicated that it took the individual animals very little time (typically, less than 2 minutes), to both get to the location where the food could be reached, and to pull it off its attachment. The same might apply for other methods that fasten the food to a certain location and just make the attainment of that location particularly challenging, including pole feeding, bungee carcasses or zip line feeding. In these scenarios, major effects – when comparing to the current baseline situation – most likely could already be attained by attaching the food more tightly, so that the attachment represents a true physical challenge rather than a negligible obstacle. Fastening the food to specific locations in the enclosure can provide variety in itself, if the different possible areas in the enclosure represent different physical challenges.

The various self-built options observed in this study that have, to our knowledge, not been widely described in the literature, bespeak considerable motivation and engagement to make feeding a challenging moment for zoo carnivores. On the other hand, the low use or lack of use of swing pole feeders, self-serving feeders or pulley feeders indicate that the published repertoire of feeding methods was not fully used by the participating institutions. In particular, the lack of feeding methods that require cooperation of social carnivores (Drea & Carter, 2009; Marshall-Pescini et al., 2017; Hare & Jones, 2018; Borrego, 2020), appears as a lost opportunity, both in terms of the attractiveness and educative potential of exhibits and in terms of effects on the social cohesion of the animal group (Fig. 2).

Arguably, the most important feature of a planned feeding regime is the variety of methods employed. In this respect, some institutions excelled, in particular for tigers, lions, lynx or brown bears (Table 5). On the other hand, the repertoire of methods available for cheetah or

wolves appeared particularly limited. Potentially, due to the anatomy of their forelimbs, these species are intuitively considered less suitable for feeding methods that require grabbing food with piercing claws and with paws in supination. Averaged across all species, 50% of institutions employed feeding on the ground/by hand only or an additional method (Table 5). Although to our knowledge studies are lacking, we consider it a well-founded intuition that an increasing number of feeding methods will foster the physical and cognitive development of zoo carnivores. At the same time, it might again enhance the attractiveness of enclosures for visitors and even incite more frequent visits. If visitors witness a pole feeding, for example, but also learn that at other times, a swinging platform feeding, a run, or a carcass hung above water might be used, they might want to witness these other methods as well. Including a variety of feeding options in the enclosure design and the management of the species may represent good husbandry practices. Evidently, sufficient work time and a consistent maintenance of the respective constructions must be factored into these plans.

A variety of feeding options might open yet another opportunity for behavioural management of zoo animals. Animals can be trained to associate certain signals with specific events. Most commonly, this occurs even involuntarily, leading to typical patterns of anticipatory behaviour once specific cues have been perceived, including time of day in regular management schedules, or sounds, looks or smells associated with food delivery. These anticipatory behaviours need not necessarily be considered negative (Watters, 2014). Actually, a study with bottlenose dolphins (*Tursiops truncatus*) indicated that the degree of anticipatory behaviour can be interpreted a measure for how much animals want to participate in a certain situation, with dolphins showing more anticipatory movement when perceiving the signal that a human would play with them compared to a signal that toys would be provided within the next half hour (Clegg et al., 2018). Transferring these observations to large carnivores, it appears plausible that once the animals have learned to associate a certain signal with a certain feeding methods (e.g. pole feeding, pulley feeder, run), they would anticipate the feeding event, which might represent a valuable cognitive enrichment for the time until feeding takes place.

In order to ensure that challenging feeding methods are not only used sporadically, but at a consistent (yet possibly randomly varying) frequency, it may be advisable to have a written management plan. Notably, an actual document does not preclude variation or flexibility, as these aspects can be included in any procedure. A written management plan should at the same time ensure that appropriate resources in terms of equipment, diet items, and work time are available, and could serve to document the degree of husbandry engagement an institution commits itself to. In particular, the absence of a written document can easily be understood by many participants as a lack of priority, a viewpoint zoos might want to avoid. The process of developing such a plan might also point out changes in construction, equipment and management necessary to meet modern expectations of carnivore feeding.

Outlook

One possibly crucial feature of natural food procurement that is lacking from feeding methods employed in zoos as outlined above is the possibility of failure – the equivalent of an unsuccessful hunting attempt. Arguably, the experience of failure, and the consequential awareness of the possibility of failure, results in a different state of mind compared to an individual that was never unsuccessful. Actually, one might argue that a 100% success rate is not success, but just a way things are – success can only exist in the face of potential failure. Therefore, denying animals the possibility of failure (as in an ‘unsuccessful feeding attempt’) might mean denying them the experience of success.

None of the visited institutions followed an outspoken strategy that included failure as an option, although some provided food in a way that required a multi-hour engagement of the animal for a successful acquisition of the food (e.g., Fig. 1F). This lack of a failure option finds its equivalent in the literature on zoo carnivore feeding. To our knowledge, the only published description of a feeding device that moves the food out of the reach of the animals if they are too slow is a pulley system designed for cheetahs (Williams et al., 1996). However, the authors did not explain whether the animals still received their food after a failed attempt, or if they were fasted for a relevant time period before the next feeding opportunity. Providing animals species-adequate physical and cognitive challenges, with a relevant failure feedback that is distinct yet not harmful, so that they are motivated to solve these challenges, could be the major future advancement of carnivore husbandry.

Acknowledgements

We thank the Felid, Canid and Hyenid TAGs for their support and sincerely thank all participating Zoos (Belgium: Antwerpen Zoo, Zoo Planckendael; Denmark: Givskud Zoo Zootopia, København Zoo, Odense Zoo, Randers Regnskov, Scandinavisk Dyrepark, Skærup Zoo; Germany: Allwetterzoo Münster, Der Grüne Zoo Wuppertal, Erlebnis-Zoo Hannover, Kölner Zoo, Serengeti Park Hodenhagen, Tiergarten Nürnberg, Tierpark Berlin, Tierpark Hellabrunn, Wingster Waldzoo, Wilhelma Stuttgart, Wisentgehege Springe, Zoo am Meer Bremerhaven, Zoo Dortmund, Zoom Erlebniswelten, Zoo Frankfurt, Zoo Heidelberg, Zoo Krefeld GmbH, Zoo Leipzig, Zoologischer Stadtpark Karlsruhe, Zoologischer Garten Schwerin, Zoo Neuwied, Zoo Osnabrück; Netherlands: Diergaarde Blijdorp, Wildlands Adventure Zoo Emmen; Norway: Dyreparken Kristiansand; Sweden: Borås Djurpark, Kolmården, Orsa Rovdjurpark, Parken Zoo, Skansen; Switzerland: Tierpark Bern, Walter Zoo, Wildnispark Zürich Langenberg, Wildpark Bruderhaus Winterthur, Zoo Basel, Zoo Zürich) and their involved staff, for their time, hospitality and participation in this study.

Zusammenfassung

Die Lebenserwartung von Raubtieren in Zoos hat sich stetig verbessert; damit stellt sich die Frage, wie diese längeren Leben verbracht werden. Weil das Fütterungsmanagement einen besonderen Einfluss auf das Verhalten von Raubtieren hat, wurde die Fütterung in 44 europäischen Zoos in sieben Ländern im Rahmen von persönlichen Besuchen erhoben. Dies erfolgte, indem die verantwortlichen Personen während ihrer täglichen Routine mit elf Raubtierarten begleitet wurden. Fleisch an Knochen wurde von der Mehrzahl der Zoos eingesetzt; eine Ganzkörper-Fütterung wurde vorwiegend mit kleinen Futtertieren (Nager, Kaninchen, Geflügel) durchgeführt, aber kaum mit größeren Tierkörpern. Während viele Zoos ein bestimmtes Repertoire an Fütterungsmethoden mit unterschiedlichem Beschäftigungspotenzial angaben, wählten die meisten Zoos während der Besuche diejenigen Methoden ihres Repertoires, die als am wenigsten arbeitsaufwändig und als am wenigsten verhaltensanreichernd einzuschätzen waren. Die Zahl der Zoos, die nur ein begrenztes Repertoire an Fütterungsmethoden angaben, war unerwartet hoch, und publizierte Methoden wie 'swing pole feeders', an Laufseilen aufgehängte Beute, oder Selbstfütterungskästen (exkl. Zeitverzögerte Futterkästen, Tonnenfütterung bei Bären) wurden in keinem der besuchten Zoos eingesetzt. Außerdem wurden weder Methoden eingesetzt, die bei sozialen Raubtieren eine Kooperation der Rudelmitglieder erfordern, noch

Methoden, bei denen die Tiere scheitern könnten (die also eine erfolglose Jagd simulieren). Um die Zoohaltung großer Raubtiere natürlichen Gegebenheiten mehr anzunähern, empfehlen wir, vermehrt die Fütterung großer Tierkörper einzusetzen, verbunden mit physisch und kognitiv adäquat herausfordernden Aufgaben; dies erfordert ggf. entsprechende bauliche und organisatorische Maßnahmen. Der regelmäßige Einsatz von aufwändigeren Fütterungsmethoden könnte durch schriftliche Einsatzpläne gesichert werden. Dadurch würden sich alle Beteiligten vermutlich auch des damit verbundenen logistischen und zeitlichen Aufwandes bewusst, wodurch eine bessere Zeiteinteilung der Abläufe zur Versorgung der Tiere entstehen kann, genügend Zeit für den Einsatz aufwändigerer Fütterungsmethoden eingerechnet wird, und eventuell notwendige Veränderungen in Bau und Ausstattung angesprochen werden.

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Appendix

Tab. A1: Methods of tigers (*Panthera tigris*) feeding in use, and personally observed (incl. the % of institutions that reported the general use of the method), at 26 zoological institutions.

Diet item	use in number of zoos	personally observed (% zoos using method)	Feeding option	use in number of zoos	personally observed (% zoos using method)	Feeding method	use in number of zoos	personally observed (% zoos using method)
Minced/processed meat	0	-	One pile for each	21	6 (29%)	Hand feeding	0	-
Organs	8	0 (0%)	Hiding	16	3 (19%)	Loose on the ground	20	11 (55%)
Whole meat	1	0 (0%)	Scattering	14	4 (29%)	Tied to the ground	18	3 (17%)
Meat on bone	26	18 (69%)	Time-delayed dispensing	2	0 (0%)	Hung up	21	7 (33%)
Whole meat with fur/feathers	0	-				Hung up with counterweight	1	0 (0%)
Carcass parts with fur/feathers	12	3 (25%)				Hung up elastic cord	8	0 (0%)
1/2 carcass	11	0 (0%)				Swinging platform	0	-
Complete eviscerated carcass	0	-				Woodpile feeder	1	1 (100%)
Carcass without digestive tract	4	0 (0%)				Swing pole feeder	0	-
Decapitated carcass	7	0 (0%)				Self-serving feeder	1	0 (0%)
Whole carcass	22	3 (14%)				Movement induced dispenser	0	-
						Feeding stick	1	0 (0%)
						Pole feeding	4	1 (25%)
						Run	0	-
						Zip line feeding	5	1 (20%)
						Pulley feeder	0	-
						Wrapped in something/hidden	14	3 (21%)
						Novel objects / self-built	8	2 (25%)
						Swimming	2	0 (0%)

Tab. A2: Methods of lions (*Panthera leo*) feeding in use, and personally observed, (incl. the % of institutions that reported the general use of the method), at 31 zoological institutions.

Diet item	use in number of zoos	personally observed (% zoos using method)	Feeding option	use in number of zoos	personally observed (% zoos using method)	Feeding method	use in number of zoos	personally observed (% zoos using method)
Minced/ processed meat	0	-	One pile for each	23	12 (52%)	Hand feeding	0	-
Organs	6	0 (0%)	Hiding	12	2 (17%)	Loose on the ground	30	12 (40%)
Whole meat	5	2 (40%)	Scattering	15	1 (7%)	Tied to the ground	18	4 (22%)
Meat on bone	31	18 (58%)	Time-delayed dispensing	1	0 (0%)	Hung up	22	4 (18%)
Whole meat with fur/feathers	10	3 (30%)				Hung up with counterweight	1	0 (0%)
Carcass parts with fur/feathers	11	0 (0%)				Hung up elastic cord	4	1 (25%)
1/2 carcass	9	2 (22%)				Swinging platform	0	-
Complete eviscerated carcass	0	-				Woodpile feeder	1	1 (100%)
Carcass without digestive tract	8	0 (0%)				Swing pole feeder	0	-
Decapitated carcass	6	1 (17%)				Self-serving feeder	0	-
Whole carcass	26	2 (8%)				Movement induced dispenser	0	-
						Feeding stick	0	-
						Pole feeding	4	1 (25%)
						Run	0	-
						Zip line feeding	5	1 (20%)
						Pulley feeder	0	-
						Wrapped in something/ hidden	11	1 (9%)
						Novel objects/ self-built	5	1 (20%)
						Swimming	0	-

Tab. A3: Methods of jaguars (*Panthera onca*) feeding in use, and personally observed (incl. the % of institutions that reported the general use of the method), at 7 zoological institutions.

Diet item	use in number of zoos	personally observed (% zoos using method)	Feeding option	use in number of zoos	personally observed (% zoos using method)	Feeding method	use in number of zoos	personally observed (% zoos using method)
Minced/ processed meat	0	-	One pile for each	2	0 (0%)	Hand feeding	0	-
Organs	1	0 (0%)	Hiding	2	2 (100%)	Loose on the ground	2	0 (0%)
Whole meat	2	0 (0%)	Scattering	2	0 (0%)	Tied to the ground	4	0 (0%)
Meat on bone	7	5 (71%)	Time-delayed dispensing	0	-	Hung up	4 (67%)	-
Whole meat with fur/feathers	0	-				Hung up with counterweight	0	-
Carcass parts with fur/feathers	3	2 (67%)				Hung up elastic cord	3	0 (0%)
1/2 carcass	1	1 (100%)				Swinging platform	0	-
Complete eviscerated carcass	0	-				Woodpile feeder	0	-
Carcass without digestive tract	1	0 (0%)				Swing pole feeder	0	-
Decapitated carcass	0	-				Self-serving feeder	0	-
Whole carcass	5	2 (40%)				Movement induced dispenser	0	-
						Feeding stick	0	-
						Pole feeding	3	1 (33%)
						Run	0	-
						Zip line feeding	1	1 (100%)
						Pulley feeder	0	-
						Wrapped in something/hidden	4	1 (25%)
						Novel objects / self-built	1	1 (100%)
						Swimming	1	1 (100%)

Tab. A4: Methods of leopards (*Panthera pardus*) feeding in use, and personally observed (incl. the % of institutions that reported the general use of the method) at 15 zoological institutions.

Diet item	use in number of zoos	personally observed (%) zoos using method)	Feeding option	use in number of zoos	personally observed (%) zoos using method)	Feeding method	use in number of zoos	personally observed (%) zoos using method)
Minced/ processed meat	0	-	One pile for each	10	3 (30%)	Hand feeding	0	-
Organs	2	0 (0%)	Hiding	4	1 (25%)	Loose on the ground	15	7 (47%)
Whole meat	2	0 (0%)	Scattering	10	1 (10%)	Tied to the ground	6	0 (0%)
Meat on bone	15	12 (80%)	Time-delayed dispensing	0	-	Hung up	12	4 (33%)
Whole meat with fur/feathers	1	0 (0%)				Hung up with counterweight	0	-
Carcass parts with fur/feathers	11	2 (18%)				Hung up elastic cord	2	0 (0%)
1/2 carcass	4	0 (0%)				Swinging platform	2	2 (100%)
Complete eviscerated carcass	0	-				Woodpile feeder	0	-
Carcass without digestive tract	3	0 (0%)				Swing pole feeder	0	-
Decapitated carcass	0	-				Self-serving feeder	0	-
Whole carcass	13	6 (46%)				Movement induced dispenser	0	-
						Feeding stick	0	-
						Pole feeding	2	0 (0%)
						Run	0	-
						Zip line feeding	1	1 (100%)
						Pulley feeder	0	-
						Wrapped in something/hidden	5	0 (0%)
						Novel objects / self-built	0	-
						Swimming	0	-

Tab. A5: Methods of snow leopards (*Panthera uncia*) feeding in use, and personally observed (incl. the % of institutions that reported the general use of the method), at 13 zoological institutions.

Diet item	use in number of zoos	personally observed (%) zoos using method)	Feeding option	use in number of zoos	personally observed (%) zoos using method)	Feeding method	use in number of zoos	personally observed (%) zoos using method)
Minced/ processed meat	0	-	One pile for each	10	7 (70%)	Hand feeding	0	-
Organs	2	0 (0%)	Hiding	5	3 (60%)	Loose on the ground	13	7 (45%)
Whole meat	1	0 (0%)	Scattering	7	1 (14%)	Tied to the ground	5	0 (0%)
Meat on bone	13	8 (62%)	Time-delayed dispensing	1	0 (0%)	Hung up	9	2 (22%)
Whole meat with fur/feathers	7	1 (14%)				Hung up with counterweight	0	-
Carcass parts with fur/feathers	0	-				Hung up elastic cord	2	1 (50%)
1/2 carcass	3	0 (0%)				Swinging platform	0	-
Complete eviscerated carcass	0	-				Woodpile feeder	0	-
Carcass without digestive tract	3	0 (0%)				Swing pole feeder	0	-
Decapitated carcass	1	0 (0%)				Self-serving feeder	0	-
Whole carcass	10	4 (40%)				Movement induced dispenser	0	-
						Feeding stick	0	-
						Pole feeding	0	-
						Run	0	-
						Zip line feeding	0	-
						Pulley feeder	0	-
						Wrapped in something/ hidden	6	1 (17%)
						Novel objects / self-built	0	-
						Swimming	0	-

Tab. A6: Methods of cheetahs (*Acinonyx jubatus*) feeding in use, and personally observed (incl. the % of institutions that reported the general use of the method), at 15 zoological institutions.

Diet item	use in number of zoos	personally observed (%) zoos using method)	Feeding option	use in number of zoos	personally observed (%) zoos using method)	Feeding method	use in number of zoos	personally observed (%) zoos using method)
Minced/ processed meat	0	-	One pile for each	14	12 (86%)	Hand feeding	1	1 (100%)
Organs	3	0 (0%)	Hiding	2	1 (50%)	Loose on the ground	15	12 (80%)
Whole meat	3	2 (67%)	Scattering	6	1 (17%)	Tied to the ground	2	0 (0%)
Meat on bone	13	4 (31%)	Time-delayed dispensing	0	-	Hung up	4	0 (0%)
Whole meat with fur/feathers	5	0 (0%)				Hung up with counterweight	0	-
Carcass parts with fur/feathers	6	0 (0%)				Hung up elastic cord	1	0 (0%)
1/2 carcass	1	0 (0%)				Swinging platform	0	-
Complete eviscerated carcass	0	-				Woodpile feeder	0	-
Carcass without digestive tract	3	2 (67%)				Swing pole feeder	0	-
Decapitated carcass	2	0 (0%)				Self-serving feeder	0	-
Whole carcass	11	4 (36%)				Movement induced dispenser	0	-
						Feeding stick	0	-
						Pole feeding	0	-
						Run	3	0 (0%)
						Zip line feeding	1	0 (0%)
						Pulley feeder	0	-
						Wrapped in something/ hidden	0	-
						Novel objects / self-built	0	-
						Swimming	0	-

Tab. A7: Methods of lynxes (*Lynx lynx*) feeding in use, and personally observed (incl. the % of institutions that reported the general use of the method), at 16 zoological institutions.

Diet item	use in number of zoos	personally observed (%) zoos using method)	Feeding option	use in number of zoos	personally observed (%) zoos using method)	Feeding method	use in number of zoos	personally observed (%) zoos using method)
Minced/ processed meat	0	-	One pile for each	16	13 (81%)	Hand feeding	2	1 (50%)
Organs	2	0 (0%)	Hiding	4	2 (50%)	Loose on the ground	15	11 (73%)
Whole meat	11	8 (73%)	Scattering	9	5 (56%)	Tied to the ground	4	0 (0%)
Meat on bone	10	6 (60%)	Time-delayed dispensing	0	-	Hung up	10	2 (20%)
Whole meat with fur/feathers	4	1 (25%)				Hung up with counterweight	0	-
Carcass parts with fur/feathers	4	0 (0%)				Hung up elastic cord	2	0 (0%)
1/2 carcass	0	-				Swinging platform	0	-
Complete eviscerated carcass	0	-				Woodpile feeder	0	-
Carcass without digestive tract	3	0 (0%)				Swing pole feeder	0	-
Decapitated carcass	0	-				Self-serving feeder	0	-
Whole carcass	15	5 (33%)				Movement induced dispenser	0	-
						Feeding stick	1	0 (0%)
						Pole feeding	3	2 (67%)
						Run	0	-
						Zip line feeding	3	2 (67%)
						Pulley feeder	0	-
						Wrapped in something/ hidden	3	0 (0%)
						Novel objects / self-built	2	2 (100%)
						Swimming	0	-

Tab. A8: Methods of hyenas (*Crocuta crocuta* & *Hyaena hyaena*) feeding in use, and personally observed (incl. the % of institutions that reported the general use of the method), at 11 zoological institutions.

Diet item	use in number of zoos	personally observed (% zoos using method)	Feeding option	use in number of zoos	personally observed (% zoos using method)	Feeding method	use in number of zoos	personally observed (% zoos using method)
Minced/ processed meat	0	-	One pile for each	11	3 (27%)	Hand feeding	1	1 (100%)
Organs	4	0 (0%)	Hiding	5	2 (40%)	Loose on the ground	11	7 (64%)
Whole meat	1	1 (100%)	Scattering	6	2 (33%)	Tied to the ground	3	0 (0%)
Meat on bone	11	7 (64%)	Time-delayed dispensing	0	-	Hung up	6	1 (17%)
Whole meat with fur/feathers	0	-				Hung up with counterweight	0	-
Carcass parts with fur/feathers	2	0 (0%)				Hung up elastic cord	0	-
1/2 carcass	0	-				Swinging platform	0	-
Complete eviscerated carcass	0	-				Woodpile feeder	0	-
Carcass without digestive tract	0	-				Swing pole feeder	0	-
Decapitated carcass	0	-				Self-serving feeder	0	-
Whole carcass	10	3 (30%)				Movement induced dispenser	0	-
						Feeding stick	0	-
						Pole feeding	0	-
						Run	0	-
						Zip line feeding	1	0 (0%)
						Pulley feeder	0	-
						Wrapped in something/ hidden	2	1 (50%)
						Novel objects / self-built	0	-
						Dug into ground	4	1 (25%)
						Swimming	0	-

Tab. A9: Methods of wolves (*Canis lupus*) feeding in use, and personally observed (incl. the % of institutions that reported the general use of the method), at 16 zoological institutions.

Diet item	use in number of zoos	personally observed (%) zoos using method)	Feeding option	use in number of zoos	personally observed (%) zoos using method)	Feeding method	use in number of zoos	personally observed (%) zoos using method)
Minced/ processed meat	1	0 (0%)	One pile for each	14	2 (14%)	Hand feeding	1	1 (100%)
Organs	6	1 (17%)	Hiding	4	0 (0%)	Loose on the ground	14	7 (50%)
Whole meat	5	2 (40%)	Scattering	7	3 (43%)	Tied to the ground	4	1 (25%)
Meat on bone	12	2 (17%)	Time-delayed dispensing	0	-	Hung up	4	0 (0%)
Whole meat with fur/feathers	2	1 (50%)				Hung up with counterweight	0	-
Carcass parts with fur/feathers	7	0 (0%)				Hung up elastic cord	0	-
1/2 carcass	2	0 (0%)				Swinging platform	0	-
Complete eviscerated carcass	0	-				Woodpile feeder	0	-
Carcass without digestive tract	2	0 (0%)				Swing pole feeder	0	-
Decapitated carcass	0	-				Self-serving feeder	0	-
Whole carcass	13	2 (15%)				Movement induced dispenser	0	-
						Feeding stick	0	-
						Pole feeding	0	-
						Run	0	-
						Zip line feeding	0	-
						Pulley feeder	0	-
						Wrapped in something/hidden	3	0 (0%)
						Novel objects / self-built	0	-
						Dug into ground	3	0 (0%)
						Swimming	0	-

Tab. A10: Methods of brown bears (*Ursus arctos*) feeding in use, and personally observed (incl. the % of institutions that reported the general use of the method), at 15 (11*) zoological institutions.

Diet item	use in number of zoos	personally observed (%) zoos using method)	Feeding option	use in number of zoos	personally observed (%) zoos using method)	Feeding method	use in number of zoos	personally observed (%) zoos using method)
Minced/ processed meat	0 (0)	-	One pile for each	11 (10)	2 (20%)	Hand feeding	0 (0)	-
Organs	4 (2)	0 (0%)	Hiding	6 (6)	1 (17%)	Loose on the ground/ thrown in	15 (11)	7 (64%)
Whole meat	8 (7)	1 (14%)	Scattering	10 (7)	4 (57%)	Tied to the ground	6 (5)	0 (0%)
Meat on bone	11 (9)	1 (11%)	Time-delayed dispensing	1 (1)	0 (0%)	Hung up	8 (3)	0 (0%)
Whole meat with fur/feathers	3 (2)	0 (0%)				Hung up with counterweight	0 (0)	-
Carcass parts with fur/feathers	4 (4)	0 (0%)				Hung up elastic cord	0 (0)	-
1/2 carcass	0 (0)	-				Swinging platform	0 (0)	-
Complete eviscerated carcass	0 (0)	-				Woodpile feeder	0 (0)	-
Carcass without digestive tract	2 (1)	0 (0%)				Swing pole feeder	0 (0)	-
Decapitated carcass	2 (2)	0 (0%)				Self-serving feeder	0 (0)	-
Whole carcass	7 (6)	0 (0%)				Movement induced dispenser	7 (5)	0 (0%)
						Feeding stick	0 (0)	-
						Pole feeding	0 (0)	-
						Run	0 (0)	-
						Zip line feeding	0 (0)	-
						Pulley feeder	0 (0)	-
						Wrapped in something/ hidden	5 (2)	1 (50%)
						Novel objects / self-built	1 (1)	1 (100%)
						Dug into ground	2 (1)	0 (0%)
						Swimming	6 (4)	1 (25%)

* Not counted are 4 institutions in which the bears were already hibernating

* According to keepers' advice, bears should be slowed down in feeding enrichment towards hibernation, therefore less different feeding methods could be personally observed

Tab.A11: Methods of polar bears (*Ursus maritimus*) feeding in use, and personally observed (incl. the % of institutions that reported the general use of the method), at 12 zoological institutions.

Diet item	use in number of zoos	personally observed (% zoos using method)	Feeding option	use in number of zoos	personally observed (% zoos using method)	Feeding method	use in number of zoos	personally observed (% zoos using method)
Minced/ processed meat	0	-	One pile for each	12	5 (42%)	Hand feeding	4	4 (100%)
Organs	5	1 (20%)	Hiding	5	3 (60%)	Loose on the ground	12	6 (50%)
Whole meat	6	1 (17%)	Scattering	7	2 (29%)	Tied to the ground	2	0 (0%)
Meat on bone	7	1 (14%)	Time-delayed dispensing	2	0 (0%)	Hung up	5	0 (0%)
Whole meat with fur/feathers	1	0 (0%)				Hung up with counterweight	0	-
Carcass parts with fur/feathers	5	0 (0%)				Hung up elastic cord	1	0 (0%)
1/2 carcass	0	-				Swinging platform	0	-
Complete eviscerated carcass	0	-				Woodpile feeder	0	-
Carcass without digestive tract	1	0 (0%)				Swing pole feeder	0	-
Decapitated carcass	1	0 (0%)				Self-serving feeder	0	-
Whole carcass	6	0 (0%)				Movement induced dispenser	0	-
						Feeding stick	0	-
						Pole feeding	0	-
						Run	0	-
						Zip line feeding	1	0 (0%)
						Pulley feeder	0	-
						Wrapped in something/ hidden	1	1 (100%)
						Novel objects / self-built	3	0 (0%)
						Dug into ground	0	-
						Swimming	3	1 (33%)

* According to keepers' advice, bears should be slowed down in feeding enrichment towards hibernation, therefore less different feeding methods could be personally observed

DER ZOOLOGISCHE GARTEN

doi:10.53188/zg0013

Zool. Garten N.F. 91 (2023) 41-46

THE ZOOLOGICAL GARDEN

Saisonalität von Geburten und Jugendmortalität und die Geburtszeit beim Südlichen Vikunja, *Lama v. vicugna* (MOLINA, 1782), in Zoos

Seasonality of births and juvenile mortality and the time of birth in southern vicunas, *Lama v. vicugna* (MOLINA, 1782), in zoos

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Zusammenfassung

Anhand der Daten aus den letzten 17 jährlich publizierten Internationalen Vikunja-Zuchtbüchern wird nachgewiesen, dass 74 % aller Vikunjageburten (Gesamtstichprobe 609) in den Zoos der nördlichen Hemisphäre in den Monaten Juli bis Oktober stattfinden. Zugleich ist die Jugendmortalität der in diesen Monaten geborenen Vikunjas mit 16 % am niedrigsten. Die Jugendmortalität der in den ersten sechs Monaten im Jahr geborenen Vikunjas betrug 36 %, diejenige der im November/Dezember geborenen 25 %. 75 % aller zeitlich erfassten 83 Vikunja-Geburten im Zoo Zürich und im Zoo Frankfurt fanden zwischen 07.00 und 13.00 Uhr statt.

Schlüsselwörter: Südliches Vikunja, Saisonalität der Geburten und der juvenilen Mortalität, Geburtszeit, Zoos der nördlichen Hemisphäre.

Einleitung

Eine erste Umfrage vom International Zoo Yearbook erbrachte zunächst gerade einmal Antworten von zwei Zoos mit sieben Vikunja-Geburten (SCHMIDT, 1973). Später kamen mehr Daten zusammen (SCHMIDT, 1975; SCHMIDT, 2006a): 67 % der 106 erfassten Vikunja-Geburten erfolgten von Juli bis Oktober. Noch ergiebiger ist die Auswertung des Internationalen Vikunja-Zuchtbuches. Dieses begann ich 1969 (SCHMIDT, 1972). Die publizierten Zuchtbücher (SCHMIDT, 1986; SCHMIDT, 1994-2002; SCHMIDT, 2006b; SCHMIDT et al., 2007; SCHMIDT & Schmidt, 2008-

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2018; SCHMIDT, 2019-2022) umfassen alle 1299 reinen Vikunjas, die von 1945 bis 2021 außerhalb der vier Heimatländer lebten.

Ergebnisse

Saisonalität der Geburten

Aus praktischen Gründen wurden für diese Studie die Jahre 2005 bis 2021 berücksichtigt, weil die entsprechenden Zuchtbücher digital vorliegen. In diesen 17 Jahren lebten außerhalb der Heimatländer nur Südliche Vikunjas, *Lama v. vicugna*. Insgesamt erfolgten 609 Einlingsgeburten, die sich auf 291 Hengste, 311 Stuten und 7 ungesexte Junges verteilen. Die Stuten waren 1 : 1,1 leicht in der Überzahl.

Von diesen 609 Vikunja-Geburten in europäischen und drei nordamerikanischen Zoos von 2005 bis 2021 fanden 451, d.h. 74 %, vom Juli bis Oktober statt. Der Prozentsatz in den einzelnen Jahren variierte relativ wenig von 62 bis 88 %. Von Januar bis Juni fanden 102 Geburten (17 %), von November bis Dezember 56 Geburten (9 %) statt (Abb. 1; Tab. 1).

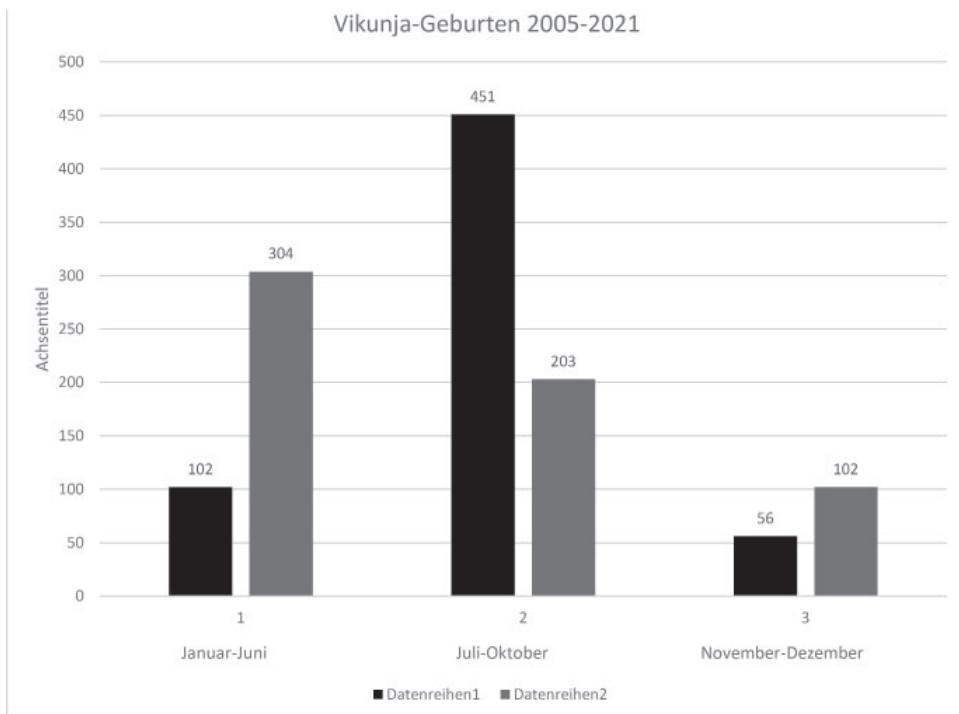


Abb. 1: Vikunjageburten in Zoos der nördlichen Hemisphäre von 2005 bis 2021. Schwarz: Zahlen aus den Internationalen Vikunja-Zuchtbüchern, grau: bei theoretisch gleichmäßiger Verteilung über das Jahr.

Fig. 1: Births of southern vicunas in zoos of the Northern hemisphere from 2005 until 2021. Black columns: numbers from the International Vicuna Studbooks, grey: columns theoretical assuming even distribution over the year.

Tab. 1: Die Zahlen zur Saisonalität der Geburten und Jugendmortalität von Südlichen Vikunjas in Zoos der nördlichen Hemisphäre von 2005 bis 2021.

Tab. 1: Numbers for the seasonality of births and juvenile mortality of southern vicunas in zoos of the Northern hemisphere from 2005 until 2021.

Saisonalität von Vikunja-Geburten und Vikunja-Jugendmortalität

Jahr	Januar-Juni Geburten	Jugendmortalität	Juli-Oktober Geburten	Jugendmortalität	November-Dezember Geburten	Jugendmortalität
2021	2,7=20 %	2,1=33 %	11,16+1=62 %	2,2+1=18 %	3,4+1=18 %	2,1+1=50 %
2020	3,6=22 %	2,0=22 %	16,13=71 %	3,2=17 %	2,1=7 %	1,0=33 %
2019	4,3=16 %	2,1=43 %	14,18=67 %	6,2=25 %	5,4=19 %	0,1=11 %
2018	3,1=10 %	2,0=50 %	12,19=76 %	1,2=10 %	4,2=15 %	2,1=50 %
2017	1,2=9 %	0	13,16=85 %	2,4=21 %	2,0=6 %	0
2016	3,2=16 %	2,0=40 %	13,13+1=84 %	2,5+1=30 %	0	
2015	3,4=24 %	1,2=43 %	6,13=66 %	1,3=21 %	3,0=10 %	1,0=33 %
2014	2,5+1=29 %	0,2+1=38 %	9,10=68 %	1,3=21 %	0,1=4 %	0
2013	1,3=12 %	0,2=50 %	11,16=82 %	1,2=11 %	1,1=6 %	0
2012	3,2=17 %	1,1=40 %	13,10=77 %	1,4=22 %	0,2=7 %	0,1=50 %
2011	1,6=18 %	1,3=57 %	16,11=71 %	1,0=4 %	1,2+1=11 %	1,0+1=50 %
2010	8,2=22 %	2,1=30 %	19,15=76 %	1,0=3 %	1,0=2 %	0
2009	4,3+1=22 %	1,3+1=63 %	12,14=72 %	1,1=8 %	1,1=6 %	0
2008	1,8=26 %	0,1=11 %	12,10=65 %	3,2=23 %	1,2=9 %	0
2007	1,1=7 %	0,1=50 %	10,11=78 %	2,1=14 %	3,1=15 %	0
2006	0,1+1=6 %	1=50 %	18,10=80 %	3,3=21 %	2,3=14 %	1,0=20 %
2005	3,0=9 %	0	14,15=88 %	1,4=17 %	0,1=3 %	0
2005-21 total	43,56+3=17 %	16,18+1=34 %	219,230+2=74 %	32,40+2=16 %	29,25+2=9 %	8,4+2=25 %
				291,311+7(56,62+7)=21 %		
	6-29 %	0-63 %	62-88 %	3-30 %	0-19 %	0-50 %

Saisonalität der Jugendmortalität

Als Jugendmortalität werden die Todesfälle in den ersten sechs Lebensmonaten gerechnet. Dies entspricht dem Ende der Säugezeit (FRANKLIN, 1976). Die Jugendmortalität zeigte ein anderes Bild als die Geburtssaison: Von den vom Juli bis Oktober – während der Geburtssaison – geborenen Vikunjas starben nur 16 % (74 Exemplare), von den vom Januar bis Juni geborenen Vikunjas 36 % (37 Exemplare) und von den im November und Dezember geborenen Vikunjas 25 % (14 Exemplare) (Abb. 2; Tab. 1). Die Jugendmortalität betrug insgesamt 21 % (125 Exemplare), diejenige der Hengste 19 % (56 Exemplare), jene der Stuten 20 % (62 Exemplare) und jene der 7 ungesexten Tiere 100 %.

Geburtszeit

Im Zoo Zürich wurden von 1964 bis 1993 die Geburtszeit von 74 Südlichen Vikunjas erfasst, von insgesamt 85 Vikunjageburten in dieser Zeitperiode. Die 11 unbekannten Geburtszeiten lagen entweder ausserhalb der Arbeitszeit von 19.00 bis 07.00 Uhr oder wurden nicht beobachtet und werden deshalb hier nicht berücksichtigt. 73 % der bekannten Geburtszeiten lagen zwischen 07.00 und 13.00 Uhr (Tab. 2). Die Geburtszeit von neun Südlichen Vikunjas im Zoo Frankfurt ergeben das gleiche Bild mit 89 % der Geburten zwischen 07.00 und 13.00 Uhr (Tab. 2). Zwischen Hengsten und Stuten war kein Unterschied in Bezug auf die Geburtszeit festzustellen.

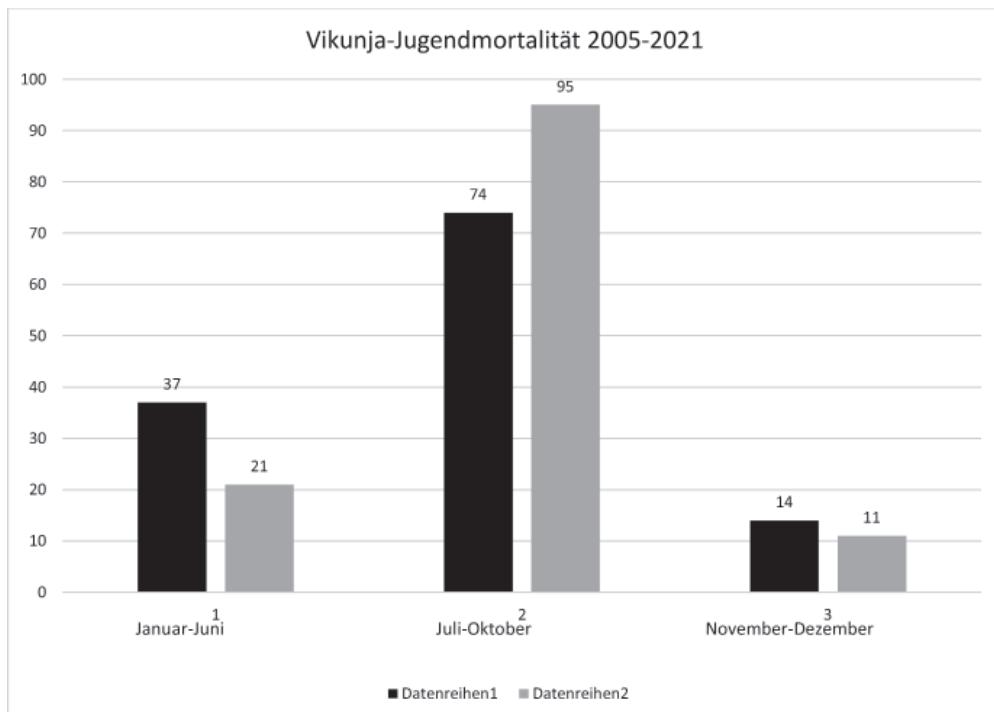


Abb. 2: Jugendmortalität von Südlichen Vikunjas in Zoos der nördlichen Hemisphäre von 2005 bis 2021. Schwarz: Todesfälle der in der angegebenen Zeit geborenen jungen Vikunjas, grau: Zahlen bei theoretisch gleichmässiger Jugendmortalität von 21 %.

Fig. 2: Juvenile mortality of southern vicunas in zoos of the Northern hemisphere from 2005 until 2021. Black columns: actual deaths of young born in the given period, grey columns: theoretical assuming evenly distributed juvenile mortality of 21 %.

Tab. 2: Geburtszeiten von Südlichen Vikunjas im Zoo Zürich von 1964 bis 1993 und im Zoo Frankfurt von 1996 bis 2004.

Tab. 2: Time of birth of southern vicunas in Zurich Zoo from 1964 until 1993 and in Frankfurt Zoo from 1996 until 2004.

07.00-10.00	10.00-13.00	13.00-16.00	16.00-19.00	total bekannt	unbekannt
18=24 %	36=49 %	15=20 %	5=7 %	74	11
3=33 %	5=56 %	1=11 %	0	9	im Zoo Frankfurt 1996-2004

Diskussion

Nach KOFORD (1957) ist März die Geburtssaison in Bolivien und Peru. Im Pampa Galeras Vikunja-Reservat erfolgten 90 % der Geburten des Nördlichen Vikunjas (*Lama v. mensalis*) zwischen dem 22. Februar und dem 7. April – die früheste Geburt war am 20.Januar, die späteste am 31. Juli (FRANKLIN, 1976). Für das Südliche Vikunja in Argentinien und Chile gibt FRANK-

LIN (2011) den Februar an. Demnach sind die hier rapportierten Geburten auf der nördlichen Erdhälfte um sechs Monate verschoben – wie zu erwarten war. Interessant ist, dass sich der Prozentsatz der Geburten vom Juli bis Oktober von 1975 (SCHMIDT, 1975) von 67 % auf heute 74 % vergrößert hat.

FRANKLIN (2011) gibt die Mortalität in den ersten vier Lebensmonaten mit 10 bis 30 % an, was der hier beschriebenen Jugendmortalität innerhalb von sechs Monaten von 21 % etwa entspricht.

FRANKLIN (1976) beobachtete 24 Geburten, wovon nur eine nicht am Vormittag war. Nach FRANKLIN (2011) erfolgten beinahe 96 % der Geburten am Vormittag. Die üblichen nachmittäglichen Stürme verunmöglichen am Nachmittag geborenen Vikunjas zu trocknen; die Mutter leckt das Junge nicht trocken. Das führt dazu, dass die Neugeborenen die kalten Nächte – bis nahe zum Gefrierpunkt – nicht überleben (FRANKLIN, 1976). Die Hauptgeburtszeit wurde in Zoos über viele Generationen – die zwölf Gründertiere (vier Hengste und acht Stuten) wurden zwischen 1946 und 1971 importiert – beibehalten, obwohl auf der nördlichen Erdhälfte andere klimatische Bedingungen herrschen.

Danksagung

Ich danke herzlich ANNEMARIE SCHMIDT für die redaktionelle, FABIAN SCHMIDT für die fachliche Überarbeitung des Manuskripts.

Summary

Data from the annually published International Vicuna Studbooks from 2005 until 2021 show that 74 % of all births in zoos of the Northern hemisphere occur from July until October (sample size 609 animals). Juvenile mortality of young born in this period is lowest with 16 %. Juvenile mortality of young born in the first six months of the year was 36 %, of those born November/December 25 %. 75 % of all timed 83 Vicuna births in Zurich Zoo and Frankfurt Zoo from 1964 until 2004 occurred between 07.00 and 13.00 hours.

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DER ZOOLOGISCHE GARTEN

doi:10.53188/zg0014

Zool. Garten N.F. 91 (2023) 47-52

THE ZOOLOGICAL GARDEN

Wegweisende Entscheidungen, die in die Gegenwart hineinwirken

Zum 100. Geburtstag von Siegfried Seifert

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Es war im Jahre 1922, als Siegfried Seifert in Rodewisch das Licht der Welt erblickte. Seine Kindheit, Jugend und das frühe Erwachsenenalter waren gezeichnet durch die Nachwehen des 1. Weltkrieges und den 2. Weltkrieg. Doch schon früh wusste der junge Seifert, dass er sich in den Dienst der Gesellschaft und für die Gesellschaft stellte, sodass er sich zum Lehrer ausbilden ließ. Wissen und Werte vermitteln, Interesse wecken und andere begeistern – das gehörte zu den selbstdefinierten Aufgaben von Siegfried Seifert. Und so wundert es nicht, dass er der Anfrage der Stadt Leipzig entsprach und am 1. September 1964 zum Zoodirektor in Leipzig berufen wurde, um für die naturwissenschaftliche Bildung und die Vermittlung der Liebe zum und das Wissen über Tiere einzutreten. Zahlreiche intensive Erfahrungen in dem Amt hatte er zuvor bereits in Rostock gesammelt, wo er zehn Jahre lang den Zoologischen Garten geleitet hatte.

20 Jahre waren seit dem 2. Weltkrieg bereits vergangen, doch die Spuren innerhalb des Leipziger Zoos waren noch deutlich sichtbar. Seiferts Aufgabe war es fortan, die Einrichtung weiterzuentwickeln und den Zoo wieder zu einem anerkannten Ort der Erholung, Bildung, Wissenschaft und des Naturschutzes zu machen. Der geneigte Zootenner weiß, dass sich diese Zielstellungen später in der Welt-Naturschutzstrategie des Weltverbandes der Zoologischen Gärten und Aquarien (WAZA) wiederfanden, den Prof. Seifert von 1991 - 1993 als Präsident führte. Zur Realisierung bedurfte es aufgrund des Zustandes des Zoos jedoch weitreichende Baumaßnahmen und Investitionen.

Am 17. März 1966 bestätigte der Rat der Stadt einen Entwurf Seiferts, der die Erweiterung des Zoogeländes, Modernisierung von Altbausubstanz und zahlreichen Neubauten enthielt.

Die beiden Raubtierhäuser und das Tieraffenhaus wurden ebenso überarbeitet wie die Bärenburg und das Elefantenhaus. Neu erbaut wurden in den Folgejahren das Vogelhaus (1969), die Huftierfreianlage am Rosental (1977) und ein Menschenaffenhaus (1982). Auch das 1910 errichtete Aquarium erfuhr unter der Leitung von Prof. Seifert eine Rekonstruktion und Erweiterung (1986). Das heutige Ringaquarium (1992) stammt in seiner ursprünglichen Fassung aus seiner Schaffensperiode.

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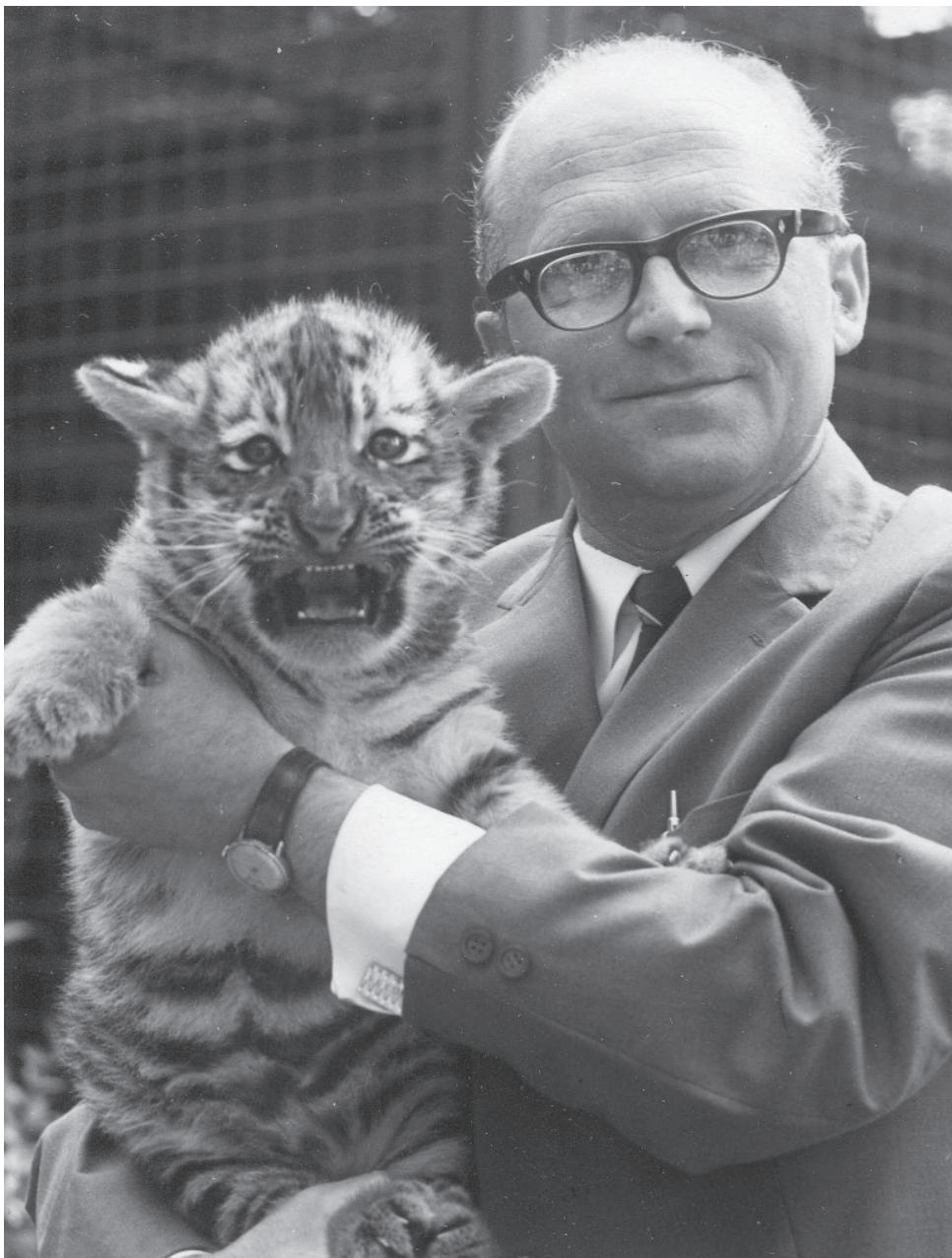


Abb. 1: Siegfried Seifert im Jahre 1978. Foto: Archiv Zoo Leipzig



Abb. 2: Siegfried Seifert im Jahre 1985. Foto: Archiv Zoo Leipzig



Abb. 3: Der Gedenkstein für Siegfried Seifert. Foto: Archiv Zoo Leipzig

Auch zoologisch erfuhr der Zoo eine Neuausrichtung. Prof. Seifert legte großen Wert auf die Haltung von Tierarten, die vom Aussterben bedroht waren. Auch verlagerte er den Schwerpunkt bei der Erhaltungszucht von den Löwen („Leipziger Löwenfabrik“) auf den stark vom Aussterben bedrohten Tiger – sein Lieblingstier. So kam es folgerichtig neben dem Bau der Tigerfarm für intensive Zuchtbemühungen auch zur Gründung des Internationalen Tigerzuchtbuches in Leipzig, das Prof. Seifert gemeinsam mit dem späteren Direktor Peter Müller 1973 aus der Taufe hob. Zahlreiche internationale Tagungen betonen die intensive Einflechtung Seiferts in internationale Gremien und die internationale Bedeutung seiner wissenschaftlichen Arbeit. Auch die Zusammenarbeit mit der damals noch Karl-Marx-Universität Leipzig heißen Hochschule wurde durch Unterzeichnung eines Rahmenvertrages intensiviert und hat heute noch Bestand. Die wissenschaftliche Arbeit war Prof. Seifert nicht nur im universitären Rahmen wichtig, sondern auch auf schulischer Ebene und in der Berufsausbildung.

So fungierte Siegfried Seifert viele Jahre als Vorsitzender bei den Facharbeiterprüfungen für Zootierpfleger, die seit den 1950er-Jahren damals wie heute zwei Mal jährlich in Leipzig stattfanden und -finden.

Auch die Gründung der Zooschule am 1. September 1969 gehört zu den bis heute nachwirkenden Leistungen von Prof. Seifert, der damit den Grundstein für den Biologie- und heute fachübergreifenden Schulunterricht im Zoo legte. Mehr als 10.000 Schülerinnen und Schüler besuchten damals wie heute jedes Schuljahr diesen spannenden und naturnahen Unterricht.

Prof. Seifert verstand es in seiner Amtszeit auch, den Zoologischen Garten Leipzig nachhaltig im gesellschaftlichen Leben zu implementieren und das Zoogeschehen auch für die Nachwelt zu bewahren. Der 1965 gegründete „Freundeskreis Leipziger Zoo“ hatte zur Aufgabe, die Öffentlichkeit bei Vorträgen, Führungen und Exkursionen zu informieren und verschiedenste Möglichkeiten zu bieten, sich aktiv über den Zoo zu bilden und in die Entwicklung einzubringen. Die erfolgreiche Arbeit des Freundeskreises zeigte sich nicht zuletzt im Anwachsen der Mitgliederzahl auf 300. Das Fundament dieser Institution wurde in den folgenden Jahrzehnten weiter genutzt und ausgebaut. Der daraus hervorgegangen „Freundes- und Förderverein des Zoo Leipzig“ ist heute noch mehr als aktiv und mit seinen Vereinsmitgliedern und Tierpaten ein wichtiger Partner des Zoo Leipzig.

Ab dem Jahr 1970 veröffentlichte der Zoo alljährlich unter dem Namen *Panthera*, ebenso wie der Jahresbericht heute noch heißt, eine Rückschau auf das zurückliegende Jahr. Mit der ersten Veröffentlichung endete eine Durststrecke von etwa zehn Jahren, in der keine Jahresberichte erschienen waren und der kompakte Überblick somit fehlt.

Diese Ausführungen machen deutlich, dass zahlreiche Jubiläen, die in den vergangenen Jahren im Zoo Leipzig gefeiert wurden und in den kommenden Jahren gefeiert werden, ohne das Schaffen und Wirken von Prof. Siegfried Seifert nicht möglich gewesen wären. Das 50. Jubiläum der Zooschule, die seit Jahren von Dr. Axel Kästner erfolgreich geleitet und inspiriert wird, der 50. Geburtstag des Freundes- und Fördervereins, der heute unter der Leitung von Präsident Michael Weichert mehr als 1.700 Mitglieder umfasst, der 50. Geburtstag des Tigerzuchtbuches im nächsten Jahr – um nur drei zu nennen.

Auch die Gestaltung des Zoogeländes weist heute noch Merkmale und Vermächtnisse des einstigen Zoodirektors auf. Vieles davon ist inzwischen erneuert und entsprechend aktueller Erkenntnisse in der Zootierhaltung und Bedürfnissen von Zoobesuchern weiterentwickelt worden. Aber die Kiwara-Savanne am Rosental, der Bärenburg-Spielplatz im Herzen des Zoos und das im Jahr 2022 modernisierte und umgebaut wiedereröffnete Aquarium zeugen von den Ideen oder dem Erhalt von historischen Anlagen in Seiferts Amtszeit.

Am 21. September 2022 wäre Prof. Siegfried Seifert 100 Jahre alt geworden. Eine lange und schwere Krankheit führte im Jahr 1998 zu seinem Tod. Sein Wirken als sechster Zoodirektor von 1964 bis 1993 im Zoologischen Garten Leipzig wirkt jedoch bis in den *Zoo der Zukunft* hinein. Wir ehren und schätzen dieses Vermächtnis!

DER ZOOLOGISCHE GARTEN

doi:10.53188/zg0015

Zool. Garten N.F. 91 (2023) 53-56

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Buchbesprechung

Buchbesprechung: Nadler, T. (2022): *Lost and found – The history of extermination, discovery and rediscovery of mammals in Vietnam. Printed in Vietnam, hardcover.* 1-615. Beziehbar bei Schueling Buchkuriert. 149 Euro.

Der Name Tilo Nadler ist eng verbunden mit dem Endangered Primate Rescue Center (EPRC) im Cuc-Phuong-Nationalpark in Vietnam, dessen Gründer er war. Der langjährige Mitarbeiter der Zoologischen Gesellschaft Frankfurt (ZGF) ist Primatologe, mit dem Spezialgebiet Languiren. Er ist Experte für das Auffangen beschlagnahmter Primaten, deren Haltung, Vermehrung sowie Auswilderung. Tilo Nadler ist auch Gründer und Herausgeber des Vietnamese Journal of Primatology. Als passionierter Artenschützer arbeitet er eng mit der Bevölkerung zusammen, ist in der Ausbildung von Rangern aktiv und setzt sich für die Erhaltung bzw. Schaffung von Schutzgebieten ein. Auch in zahlreiche Säugetierentdeckungen war Tilo Nadler bereits involviert, so hat er bereits vor 25 Jahren den Grauschenkligen Kleideraffen (*Pygathrix cinerea*) wissenschaftlich beschrieben – und zwar in dieser Zeitschrift (Nadler, 1997). Zahlreiche Publikationen und Bücher vor allem zu Vietnams Primaten machen das beeindruckende Lebenswerk von Tilo Nadler aus.

Sein jüngstes Werk hat Tilo Nadler der faszinierenden Säugetierwelt Vietnams gewidmet, und zwar insbesondere den Säugetierarten, die entweder mittlerweile als ausgerottet gelten oder besondere Entdeckungs- bzw. Wiederentdeckungsgeschichten haben. Auch Säugerarten, deren Systematik in den letzten 30 Jahren signifikante Veränderungen erfahren haben, werden abgehandelt. Und zu all dem gibt es aus Vietnam mehr als reichlich zu berichten, worauf bereits die über 600 Seiten (!) dieses Buches verweisen. Die Titelseite des attraktiv aufgemachten, mit einem grün glänzenden Lesebändchen versehenen Buchs weckt bereits Interesse zum Nachlesen, sind dort doch bereits 14 der spannendsten Arten abgebildet.

Nach jeweils einseitigem Vorwort, Danksagung und Einleitung kommt es rasch zum Hauptteil des Buchs, den Artkapiteln zu den 12 Säugetierordnungen. Vorab werden diese kurz vorgestellt, es folgt eine Artenliste für Vietnam und am Ende folgt die Spezialliteratur zur Ordnung. Kernstück sind die zumeist mehrseitigen Artabhandlungen, die nach Vorstellung des englischen und wissenschaftlichen Namens samt Erstbeschreiber und Beschreibungsjahr ausführlich auf Entdeckung, Verbreitung und Status eingehen. Dies ist schon spannend genug, doch werden zusätzlich zu den Artbildern auch die Entdecker – sofern Portraits verfügbar waren – abgebildet und in einem Infokasten kurz vorgestellt. Dazu gibt es auch noch Verbreitungskarten und allerlei Besonderheiten, ob nun Briefmarken mit Artportraits, historische Fotos oder Dokumentationen. Zu Letzteren zählen auch die Abbildungen der Originalbeschreibungen insbesondere von bereits vor längerer Zeit beschriebenen Taxa.

Das alles macht das Buch nicht nur für den interessierten Laien, sondern auch für den Experten hoch interessant. Zusätzlich gibt es, zwischen den Artabhandlungen eingestreut, auch Kapitel, in denen besondere Persönlichkeiten und ihre Erfahrungen in Wort und Bild dargestellt

werden, angefangen vom Autor des Buches selbst über seine WeggefährtInnen wie z. B. die Veterinärin Ulrike Streicher bis hin zu ehemaligen Wilderern, wie Tran Kim Lieu, der nachfolgend zu einem Artenschützer wurde – und natürlich zu bekannten Zoologen aus Vietnam, wie z. B. Prof. Vo Quy (1929-2017), der sowohl mir im Rahmen meiner Doktorarbeit als auch dem Kölner Zoo bei den ersten Schritten in Vietnam half.

Obwohl ich jetzt selbst schon seit über 25 Jahren in und zu Vietnam forsche und mich gemeinsam mit den vietnamesischen KooperationspartnerInnen für den Erhalt der dortigen Artenvielfalt einsetze – also schon einiges selbst gesehen, gehört und gelesen habe –, hat mich dieses Buch voll in seinen Bann gezogen. Das Spektrum der vorgestellten Wissenschaftler reicht von Linnaeus (1707-1778), dem Begründer der modernen zoologischen Nomenklatur, bis zu den heute noch in Vietnam aktiven Säugetierforschern aus aller Welt. Angefangen von A wie Alexander Olegovich Averianov, Säugetierkundler am Zoologischen Institut der Russischen Akademie der Wissenschaften in St. Petersburg, der Erstbeschreiber des Annam-Streifenkaninchens (*Nesolagus timminsi*), über René Léon Bourret (1884-1957), Professor der Université Indo-chinoise in Hanoi (Vietnam), der primär als Herpetologe bekannt wurde, aber auch Säugetiere aus Vietnam entdeckt und beschrieben hat, bis zum deutschen Naturwissenschaftler Eberhard August Wilhelm von Zimmermann (1743-1815), der 1780 den Schweinhirsch (*Axis porcinus*) beschrieben hat. Die Kurzporträts bekannter historischer Größen, die dank Zeichnungen oder Fotos ein Gesicht bekommen, faszinieren. So z. B. der Niederländer Johan C. van Hasselt, dessen Namen sich in der Wirbeltierwelt Südostasiens vielfach wiederfindet, dessen Porträt allerdings ein tragisches Schicksal wiedergibt – van Hasselt fiel im jungen Alter von nur 26 Jahren nach nicht einmal drei Jahren Sammeln und Forschen auf Java den Tropen zum Opfer. Aber auch vielen in Vietnam tätigen ForscherkollegInnen, die ich bisher noch nicht getroffen hatte, konnte ich hier dank der Porträts sozusagen das erste Mal persönlich begegnen.

Zusätzlich ziehen einen natürlich die Entdeckungsgeschichten in ihren Bann, so z. B. der Lazaruseffekt bei der Laotischen Felsenratte (*Laonastes aenigmamus*). Die Entdeckungen wie die der Saola oder Vu-Quang-Antilope (*Pseudoryx nghetinhensis*) machen aber auch betroffen, denn man kann nur hoffen, dass es noch Exemplare in freier Wildbahn gibt. Und der Autor hat sich wirklich Mühe gegeben, sämtliche verfügbaren Details zusammenzutragen. Dem 1937 beschriebenen Kouprey (*Bos sauveli*) sind allein zwölf Seiten gewidmet, einschließlich Zeichnungen, Trophäen, historischen Abschluss- und Lebendbildern. Dieses Wildrind dürfte allerdings nicht mehr existieren. Auch das Vietnamesische Nashorn (*Rhinoceros sondaicus annamiticus*) hat vor nicht allzu langer Zeit im Cat-Tien-Nationalpark dank menschlichen Dazutuns das Ende seiner Existenz gefunden. Insofern ist das Buch nicht nur ein Rückblick, sondern hält uns, wenn auch dezent und versteckt, ebenfalls einen Spiegel vor, nämlich dass das, was wir ausgerottet haben, nicht mehr wiederkehrt und wir deshalb unsere Verhaltensweisen und ihre Konsequenzen ernsthaft überdenken sollten. Sozusagen als Mahnmal sind für den Indochinesischen Tiger (*Panthera tigris corbetti*) u. a. die letzten Sichtungen, aber auch Attacken, Fallenfänge und Abschüsse nach Jahreszahlen sortiert gelistet.

Immer noch kurios und als wissenschaftlicher Fall noch nicht völlig abgeschlossen ist die Geschichte der Spiralhornantilope, auch Khting Vor genannt (*Pseudonovibos spiralis*), über die Tilo Nadler und ich u. a. zusammen mit einem der Erstbeschreiber, Dr. Alfred Feiler, ehemaliger Kustos am Tierkundemuseum Dresden, vor über 20 Jahren schon gemeinsam publiziert haben, „Mythos oder Wirklichkeit“ (Feiler et al. 2002). Die Liste an Entdeckungen reicht bis in die Neuzeit, so ist auch das erst vor fünf Jahren entdeckte Hon-Khoai-Hörnchen (*Callosciurus honkhoaiensis*) mit dabei. Ich selbst hatte ja 1997 auch einmal das Glück, eine Säugetierart zu entdecken, die ebenfalls vorgestellte, von Lunde et al. (2004) wissenschaftlich beschriebene Ke-Go-Weißzahnspitzmaus (*Crocidura kegoensis*). Und dieser Fall zeigt auch anschaulich, dass Forschung im steten Wandel ist und dass Vietnam immer noch für Überraschungen in Sachen

Entdeckungen gut ist. Denn eine ganz aktuelle, kurz nach dem vorliegenden Buch erschienene genetische Studie hat erwiesen, dass diese jahrzehntelang als Endemit für die Provinz Ha Tinh geglaubte Art – also nur dort in Vietnam vorkommend – tatsächlich auch an anderen Stellen dieses Landes zu finden ist. Und die drei Jahre später beschriebene Zaitsevs Weißzahnspitzmaus (*C. zaitsevi*), die im Buch noch als eigene Art geführt ist, stellt seit neuestem ein Synonym von *C. kegoensis* dar, ist also gar keine eigenständige Art (Bannikova et al., 2022). Es bleibt also nicht nur spannend, in diesem Werk zu schmökern, sondern sich danach auch überraschen zu lassen, was die Zukunft an neuen Informationen und hoffentlich positiven Überraschungen noch so bringen wird.

Bei solch einem Opus bleibt der eine oder andere Fehler natürlich nicht aus, so werden die Spitzhörnchen als Scadentia (statt als Scandentia) vorgestellt, doch ist das angesichts der Informationsfülle dieses Buches und der wirklich sehr detaillierten Recherche des Autors absolut vernachlässigbar. Das Buch endet nach gefühlt unzähligen Artkapiteln und Forscherportraits mit einem Index der fast 200 Biographien und den umgangssprachlichen und wissenschaftlichen Namen der abgehandelten Säugetierarten.

Man kann es meiner Rezension ja bereits entnehmen, dass mich das Buch überzeugt und in seinen Bann gezogen hat. Ich kann es daher jedem, der an Säugetieren, Vietnam, aber auch an Entdeckungsgeschichten generell interessiert ist, nur empfehlen. Vietnam hat diesbezüglich auch wirklich außerordentlich viel – ob nun Historisches, Aktuelles, Mythologisches oder spektakuläres – zu bieten.

Summary

Tilo Nadler, founder of the Endangered Primate Rescue Center (EPRC) in the Cuc Phuong National Park in Vietnam and longtime employee of the Frankfurt Zoological Society (FZS) is a primatologist and passionate conservationist. He was also involved in numerous discoveries of mammals, for example he described the grey-shanked douc langur in this journal (Nadler 1997). Numerous publications, especially on Vietnam's primates, make up his impressive life's work. His most recent work is dedicated to the mammal fauna of Vietnam, namely those that are either now considered extinct, have special stories of discovery or rediscovery, or whose systematics have changed significantly in the last 30 years. After each one-page foreword, acknowledgments and introduction, the species chapters for the 12 orders of mammals follow. The orders are presented briefly together with a species list for Vietnam, followed by the special literature at the end. The main part here are the mostly multi-page species essays that go into detail about discovery, distribution and status. In addition, the discoverers are also shown and briefly introduced. There are also distribution maps and special features such as historical photos or the original descriptions of the species. All this makes the book highly interesting not only for the interested layman but also for the expert. In addition, there are also chapters in which special personalities from Vietnam or who work there and their experiences are presented in words and pictures. The spectrum of presented scientists ranges from Linnaeus, the founder of modern zoological nomenclature, to the mammal researchers from all over the world who are still active in Vietnam today. The short portraits of both well-known historical personalities and acting mammalogists, who are given a face thanks to drawings or photos, are fascinating. In addition, of course, the very well researched stories of discovery are fascinating, e.g. that of the Laotian rock rat (*Laonastes aenigmamus*) and the Lazarus effect. However, the discoveries such as those of the saola (*Pseudoryx nghetinhensis*) are also concerning, because it is not known whether there are still free-living individuals. Twelve pages alone are dedicated to the kouprey (*Bos sauveli*), which was described in 1937 and is now probably extinct, including drawings, trophies, historical kills and living images. The Vietnamese rhino (*Rhinoceros sondaicus annamiticus*)

was also recently wiped out with the death of the last individual in Cat Tien National Park. In this respect, the book is not only a retrospective, but also holds up a mirror to us with our destructive actions and urges us to reflect. The history of the Khting vor (*Pseudonovibos spiralis*), about which we jointly published more than 20 years ago: "Myth or reality" (Feiler et al. 2002), is still curious and not yet completely closed as a scientific case. The book also contains the Hon Khoai squirrel (*Callosciurus honkhoaiensis*) which was only recently discovered. In 1997 I was fortunate enough to discover a species of mammal, the Ke Go white-toothed shrew (*Crocidura kegoensis*) described by Lunde et al. (2004), likewise presented in the book. And this discovery also clearly shows that research is constantly changing. A genetic study that has just been published has shown that the Ke Go white-toothed shrew, which for decades was believed to be endemic to Ha Tinh Province, can actually be found in other parts of the country. And the Zaitsev's white-toothed shrew (*C. zaitsevi*), described three years later, which is still listed as a separate species in the book, has recently become a synonym of the Ke Go white-toothed shrew (Bannikova et al. 2022). With such an opus, one or the other error is of course inevitable, for example the treeshrews are presented as Scadentia (instead of Scandentia), but in view of the wealth of information this is absolutely negligible. The book concludes with an index of nearly 200 biographies and the names of the mammal species discussed. I highly recommend this fascinating book to anyone interested in mammals, Vietnam but also history of discovery. Vietnam really has a lot to offer in this respect – whether historical, current, mythological or spectacular reports.

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Prof. Dr. Thomas Ziegler

DER ZOOLOGISCHE GARTEN

doi:10.53188/zg0016

Zool. Garten N.F. 91 (2023) 57-78

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Husbandry, feeding, veterinary and reproductive management in maned wolves (*Chrysocyon brachyurus*) in zoological facilities in Europe, Australia and North America

Haltung, Fütterung, tiermedizinisches und Fortpflanzungsmanagement von Mähnenwölfen (*Chrysocyon brachyurus*) in europäischen, australischen und nordamerikanischen Zoos

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Abstract

Historically, the zoo-kept maned wolf (*Chrysocyon brachyurus*) population has suffered from poor reproductive success and a high prevalence of cystinuria, which was attributed to the feeding of a carnivore diet to these generalist omnivores. A multi-institutional survey of zoos ($n=62$) in Europe, North America and Australia was conducted to evaluate relationships between husbandry, feeding, reproduction and medical management. Data was collected on 169 animals, 81 females, 86 males and two of unknown sex, ranging in age from 1 month to 16 years. This study indicates that factors relevant to reproductive success include paternal parenting behaviour, restricting access to indoor enclosures, the presence of previous offspring during the breeding season and insufficient monitoring during the reproductive period. Health concerns most frequently reported over the past 15 years were poor body condition, cystinuria and nephritis. Diets varied considerably, with North American zoo diets typically including Mazuri®

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Maned Wolf Diet or commercial dog foods, and European and Australian zoo diets primarily consisting of small prey animals with varying additions of fruit and vegetables. The most notable difference between all zoo diets and the diet of free-ranging maned wolves was a lack of grasses and *Solanum* fruits in zoo diets. The findings in this study suggest that zoo diets would mirror the diets of free-ranging animals more effectively if they contained equal proportions of animal and plant material, which could potentially also help to address poor body condition and cystinuria. To address the poor reproductive success, further research, including close monitoring during the reproductive period, is warranted.

Keywords: Maned wolf, *Chrysocyon brachyurus*, feeding, husbandry, reproduction, diseases

Introduction

Maned wolves (*Chrysocyon brachyurus*) have been kept in zoos in Europe and the United States since the 1960s (Dmoch, 2007). In the United States, the Maned Wolf Species Survival Plan (MWSSP) manages the captive population of maned wolves and works together with similar programmes in other regions of the world, such as the European Ex-situ Programme (EEP), to sustain genetic diversity and improve the collective understanding of maned wolf husbandry (Songsasen & Rodden, 2010). There are currently 66 zoological institutions in Europe housing maned wolves, 33 in North America and 7 in Australia (Holland, 2020). The total population has been increasing, but the numbers have been stagnating in recent years (Fig. 1). The main challenge of maned wolf husbandry is poor reproduction, which is reflect-

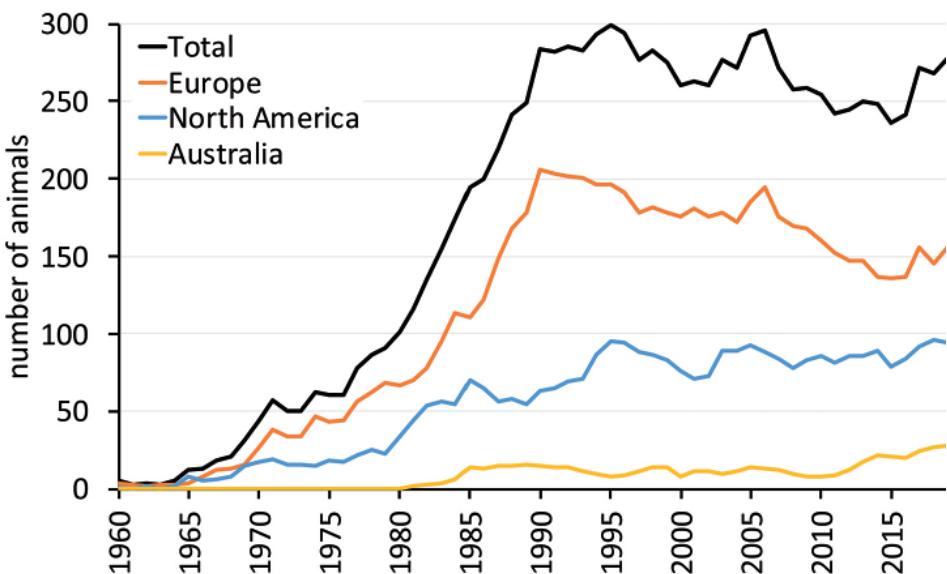


Fig. 1: Population development of the total global population of zoo-kept maned wolves including Asia, South America, North America, Europe and Australia, as well as the individual population development in North America, Europe and Australia (Holland 2020).

ed in the global as well as regional population pyramids, which lack a broad basis of neonates and juveniles, possibly except for the European population (Fig. 2). Additional challenges comprise appropriate feeding regimes and some health issues, especially cystinuria (Songsasen & Rodden, 2010).

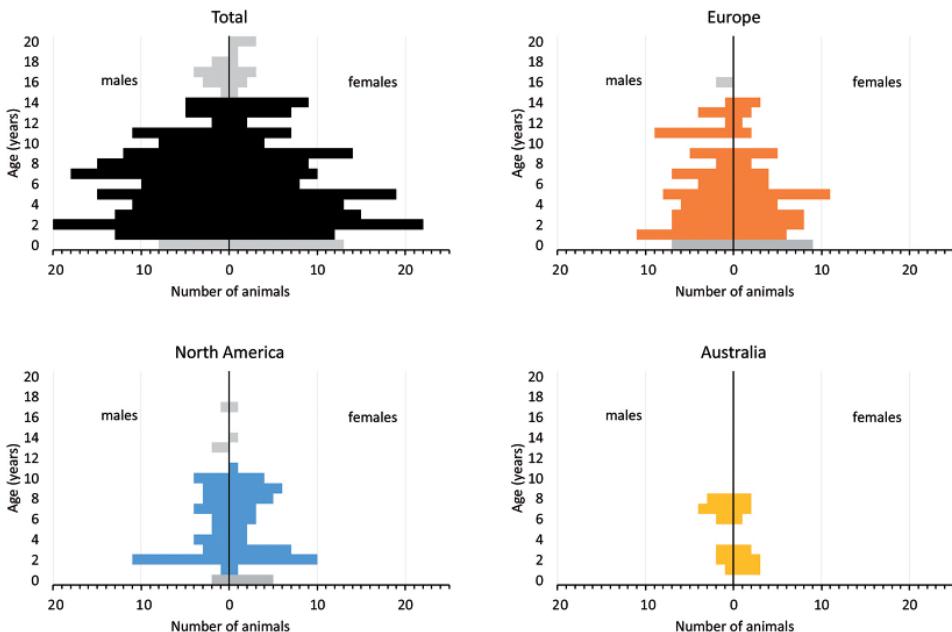


Fig. 2: Age distribution of the total global population of zoo-kept maned wolves including Asia, South America, North America, Europe and Australia, as well as the individual age distribution in North America, Europe and Australia (Holland 2020). Animals over the age of 15 are potentially no longer alive, however, their deaths have not been registered in Species360 Zoological Information Management System (ZIMS) for Studbooks (Holland, 2020).

Free-ranging maned wolves have been classified as generalist omnivores, consuming on average 50% plant material and 50% vertebrates and invertebrates, with some variation between habitats and the wet and dry season (Fig. 3). The plant material most commonly consumed by the maned wolf in its native habitat is *Solanum lycocarpum*, known locally as lobeira or “wolf’s fruit” (Dietz, 1984; Lombardi & Junior, 1993; Courtenay, 1994; Motta-Junior & Martins, 2002). *Solanum* species make up the second largest proportion of the biomass consumed by maned wolves, only surpassed by vertebrate prey (Motta-Junior et al., 1996; Bueno et al., 2002; Bueno & Motta-Junior, 2004; de Arruda Bueno & Motta-Junior, 2009).

The formulation of an appropriate diet for maned wolves in zoos is considered to be a major challenge (Songsasen and Rodden 2010), especially because they often appear to respond to minor dietary changes with diarrhoea and poor body condition (Bush 1980). In the 1980s, maned wolves in US zoological institutions were often fed the same raw, meat-based diets normally fed to exotic felids (Rodden et al. 2007). Since then, captive maned wolves in US zoos have been commonly fed diets based on formulations for domestic dogs (*Canis lupus familiaris*) (Songsasen and Rodden 2010).

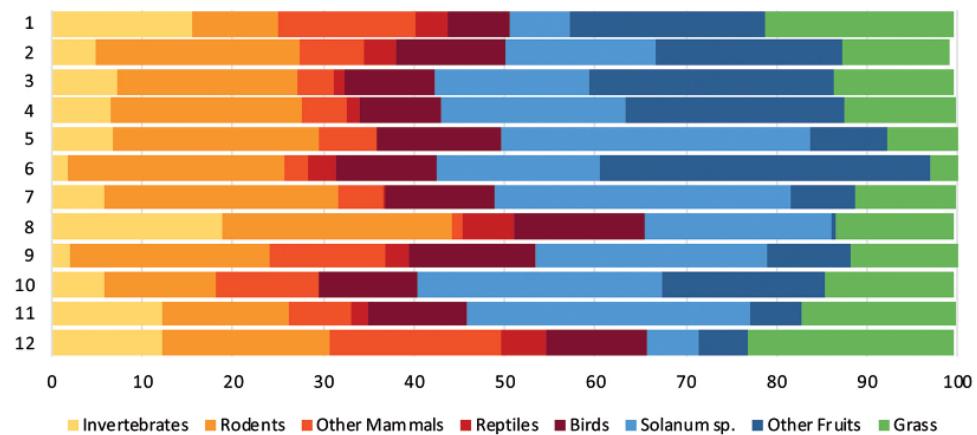


Fig. 3: Proportion of invertebrates, rodents, other mammals, reptiles, birds, *Solanum* sp., other fruits and grass in the diet of free-ranging maned wolves (*Chrysocyon brachyurus*) from various studies. 1 (Aragona & Setz, 2001), 2 (Bueno et al., 2002), 3 (Bueno & Motta-Junior, 2004), 4 (de Arruda Bueno & Motta-Junior, 2009), 5 (Carvalho & Vasconcellos, 1995), 6 (de Almeida Jácomo et al., 2004), 7 (Dietz, 1984), 8 (Massara et al., 2012), 9 (Motta-Junior et al., 1996), 10 (Rodrigues et al., 2007), 11 (Santos et al., 2003), 12 (Silva & Talamoni, 2003).

The most prominently discussed health issue in maned wolves has long been cystinuria, which has been reported in both free-ranging and zoo-kept animals (Bush & Bovee, 1978; Bovee et al., 1981; Mussart & Coppo, 1999). Cystinuria is characterised by elevated levels of cystine in the urine, which can result in the formation of calculi in the kidneys and bladder and thereby cause clinical symptoms (Songsasen & Rodden, 2010). To address the link between meat-based diets and cystinuria, a maned wolf diet that was intended to reduce and prevent cystinuria was formulated in 1998 (Boniface, 1998). The specific maned wolf diet reduced the concentration of cystine in the urine significantly in a sample of four maned wolves and was subsequently modified to include more plant protein instead of animal protein to increase urinary pH (Childs-Sanford, 2005). The feeding of this specific maned wolf diet was discontinued in the US in 2002, after concerns that it could have a negative impact on reproduction, and the feeding of dog food supplemented with fruits, vegetables and small whole prey items recommenced (Songsasen & Rodden, 2010). A survey carried out in 24 US zoos in 2006 found that 15 different brands of dog food were being fed, and there was great variation in the amount and type of fruits, vegetables and whole prey items supplemented. However, no correlations between diet, health and reproductive success could be determined from this survey (Songsasen & Rodden, 2010). Thus, many questions about optimal feeding and health management for maned wolves still remain unanswered.

The reproduction of maned wolves has proven to pose the most significant challenge to the successful maintenance of populations in zoos. In 2010, the target population in North America was 100 maned wolves. Between 2003 and 2007, the population always remained at around 95 animals. However, in 2008 and 2009 reproduction was inexplicably poor and the population dropped to 80 individuals (Songsasen & Rodden, 2010). Historical data from 1982–1998 showed that 53% of pups were lost in the first year and 78% of those deaths occurred in the first 30 days. Of the deaths in the first 30 days, 88% were classified as ‘parental incompetence’, which included pups being devoured, neglected, attacked by the dam or sire, going missing or being stillborn (Maia & Gouveia, 2002). Maned wolves are highly seasonal breeders (Heldstab

et al., 2018) and give birth in the winter season of the respective hemisphere (Fig. 4), which may make the raising of young particularly challenging. In the United States, only 38% of 166 recommended breeding pairs produced pups between 1996 and 2007, 50% of pregnant females losing neonates within a few days after birth (Songsasen & Rodden, 2010). A study by Reiter (2012) indicated a relationship between pup mortality and elevated levels of faecal corticoids, thus suggesting stressors such as poor health and suboptimal enclosures could be causes for neonatal losses. In the Maned Wolf Husbandry Manual from 2007, it is therefore recommended to provide multiple den sites to breeding pairs to reduce stress and install video cameras to closely monitor pregnant females (Rodden et al., 2007). Velloso et al. (1998) found that the reproductive cycle of female maned wolves is reflected in faecal steroid concentrations and therefore suggested testing faecal samples to determine pregnancy in order to prepare more effectively for whelping and potentially reduce the occurrence of infanticide. The true causes of poor reproductive success in maned wolves are unknown and require further investigation.

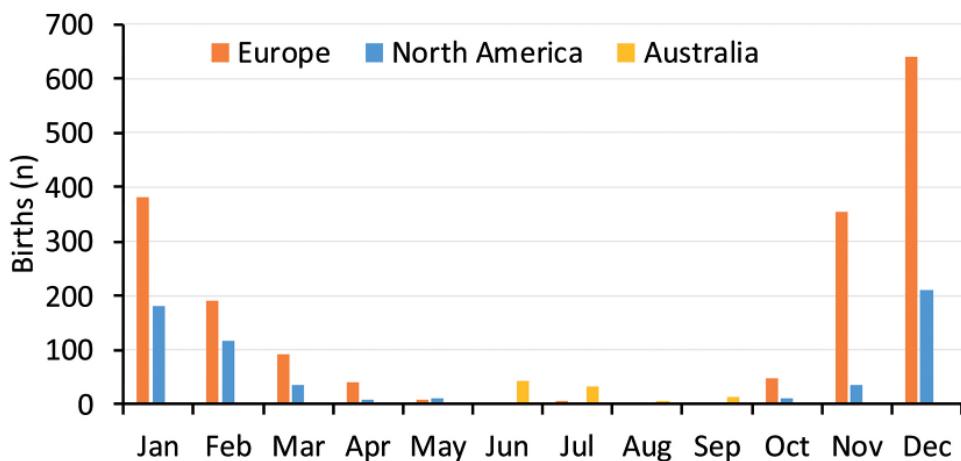


Fig. 4: Birth of zoo-kept maned wolves in Europe, North America and Australia (Holland, 2020).

The aims of this study are to further investigate the causes of poor reproductive success in maned wolves kept in zoos, as well as getting an overview over the main diseases that are currently relevant in the zoo-kept population and the current development of feeding practices. Due to the fact that poor reproduction is a main concern in maned wolf husbandry, data displayed in tables is separated into all institutions and institutions with breeding pairs with and without recent offspring (between 2017-2021).

Materials and methods

This study used a survey to collect information on maned wolf husbandry. The details asked in the questionnaire are evident from the result tables; the original questionnaires can be requested from the corresponding author. Forty-three facilities with a total of 111 maned wolves in Europe and Australia participated in this study. Previously unpublished data collected from 58 animals in 19 zoos in the United States from 2017 to 2018 was also made available for this study by the nutrition advisor of the Association of Zoos and Aquaria's (AZA) Canid Taxon Advisory Group (TAG). As the zoos did not all provide answers con-

sistently to all questions, the number of facilities for which a specific answer was noted varied between questions.

Of the participating facilities in Europe, only six were visited personally over the course of 2020 due to the travel restrictions during the COVID-19 pandemic. In these facilities, interviews were conducted with curators and/or keepers to gather information on husbandry, feeding, enrichment, medical practices and, where relevant, reproduction. Additionally, any available post-mortem reports were collected for evaluation, the behaviour of the animals was observed, and photos were taken for body condition scoring, to score faeces consistency and to document enclosures. All facilities that could not be visited received a survey containing questions concerning husbandry, feeding, enrichment, medical practices and, where relevant, reproduction. Supplementary data for all zoos was collected by the second author (the studbook coordinator) using the Species360 Zoological Information Management System (ZIMS) for Studbooks.

Descriptive statistics concerning husbandry, feeding, health and reproduction were calculated for the total population surveyed, as well as for institutions with breeding pairs with recent offspring (between 2017–2021) and without recent offspring (between 2017–2021). The statistical analyses used in the software R (R Core Team, 2020) were the chi-squared test and the Wilcoxon signed-rank test functions. No corrections were applied for multiple testing; due to the very large number of statistical tests, these should all be considered exploratory.

Results

Husbandry

The mean number of animals per institution was 2.65, and facilities with breeding pairs with recent offspring had – as expected – significantly more animals than zoos without recent offspring (Table 1). The mean indoor enclosure size per institution was 25 m² and the mean outdoor enclosure size 1,459 m². Indoor enclosures were defined as a building with one or more boxes inside. The mean indoor enclosure size available per animal was 13 m² and the mean outdoor enclosure size available per animal was 557 m². Ten of the 62 zoos (16%) did not have indoor enclosures. Instead, these zoos offered only dens in the outdoor enclosure as shelters for the animals. Zoos with no indoor enclosure had a mean number of two outdoor shelters. Zoos with indoor enclosures also had a mean number of two outdoor shelters and additionally had a mean number of 2 indoor shelters.

38 (61%) of the zoos participating in this study had a breeding pair at the time of the survey and 24 (39%) did not. Ten (26%) of the zoos with breeding pairs and seven (29%) of the zoos without breeding pairs reported having more than one outdoor shelter per animal. Of the 32 (84%) zoos with breeding pairs that had an indoor enclosure, eight (25%) reported having more than one indoor shelter per animal. Of the 20 (83%) zoos without breeding pairs that had an indoor enclosure, nine (45%) reported having more than one indoor shelter per animal. The mean temperature in the indoor enclosures or dens (if heated) in winter was 17 °C. Nine zoos (15%) locked their maned wolves in overnight. 19 zoos (31%) locked their maned wolves out during the day in order to increase visibility to visitors, and this was done significantly more frequently among zoos without breeding pairs with recent offspring (Table 1) – possibly, because these zoos had less animals in total.

Data were collected for 84 male and 78 female maned wolves, the groupings of which are further detailed in Figure 5. 24 zoos reported having had same-sex housing either currently or in the past. Of these, 17 (71%) reported male only groups and 9 (38%) reported female only groups. 17 (71%) of these groupings were siblings. All male only groups were reported to have

Tab. 1: Parameters surveyed concerning enclosures and husbandry analysed for all facilities, facilities with breeding pairs with recent offspring (between 2017-2021) and facilities with breeding pairs without recent offspring (between 2017-2021).

	All facilities	Facilities with breeding pairs with recent offspring	Facilities with breeding pairs without recent offspring
	mean ± standard deviation (range; n)		
Number of animals per zoo	2.65 ± 2.43 (0-15; 62)	4.26 ± 3.11 ^a (2-15; 23)	2.20 ± 1.37 ^b (1-7; 15)
Outdoor enclosure (m²)	1459 ± 1743 (185-11409; 60)	2194 ± 2528 (230-11409; 23)	1182 ± 918 (185-4000; 15)
Number of zoos with < 930 m²	27 (45%)	9 (39%)	6 (40%)
Number of zoos with > 930 m²	33 (55%)	14 (61%)	9 (60%)
Indoor enclosure (m²)	25 ± 18 (3-100; 44)	31 ± 24 (10-100; 18)	24 ± 13 (9-60; 12)
Mean outdoor size per animal (m²)	557 ± 402 (77-2300; 60)	553 ± 524 (77-2300; 23)	525 ± 234 (103-1000; 15)
Mean indoor size per animal (m²)	13 ± 10 (2-50; 44)	11 ± 12 (2-50; 18)	13 ± 9 (5-30; 12)
Indoor enclosure available	52 of 62 (84%)	19 of 23 (83%)	13 of 15 (87%)
Number of outdoor shelters	2 ± 1 (0-6; 60)	2 ± 1 (0-6; 23)	2 ± 1 (0-4; 15)
Outdoor shelters per animal	1 ± 1 (0-3; 60)	1 ± 1 (0-3; 23)	1 ± 1 (0-3; 15)
Number of indoor shelters	2 ± 1 (0-5; 36)	2 ± 1 (0-4; 14)	2 ± 2 (0-5; 7)
Indoor shelters per animal	1 ± 1 (0-3; 36)	1 ± 1 (0-2; 14)	1 ± 1 (0-3; 7)
Average winter temperature of indoor enclosure or dens (°C)	17 ± 3 (7-24; 38)	18 ± 4 (10-24; 15)	16 ± 4 (7-20; 8)
Locked in over night	9 (of 61; 15%)	3 (of 23; 13%)	1 (of 15; 7%)
Locked out during the day	19 (of 61; 31%)	5 (of 23; 22%) ^c	8 (of 15; 53%) ^d
Time spent indoors in winter (hours per day)	15 ± 5 (0-21; 37)	14 ± 5 (0-21; 15)	14 ± 6 (5-20; 7)
Time spent indoors in summer (hours per day)	8 ± 5 (0-20; 37)	10 ± 5 (1-20; 15)	8 ± 5 (0-14; 7)
Time spent outdoors in winter (hours per day)	9 ± 5 (3-24; 37)	10 ± 5 (3-24; 15)	10 ± 6 (4-19; 7)
Time spent outdoors in summer (hours per day)	16 ± 5 (4-24; 37)	14 ± 5 (4-23; 15)	16 ± 5 (10-24; 7)

^{a-b} Means with different superscript letters differ significantly ($p<0.05$) for successful and unsuccessful breeding pairs for the given parameter (Wilcoxon test).

^{c-d} Percentages with different superscript letters differ significantly ($p<0.05$) for successful and unsuccessful breeding pairs for the given parameter (chi-square test).

worked well, whereas two (22%) of the nine female groups were reported to fight, leading to injuries. In one of these groups, the animals were siblings and in the other they were not.

Five zoos had a mixed exhibit at the time of survey, four with giant anteaters and one with tapirs. Two (40%) of the mixed exhibits housed breeding pairs together with giant anteaters. One of the breeding pairs reproduced successfully, the other did not. The other three (60%) mixed exhibits did not house breeding pairs. Two zoos reported having previously successfully housed maned wolves with other species, one with capybaras and one with llamas. These zoos did not have a breeding pair at the time and specified that they believed the mixed exhibit could only be successful as long as neither species had offspring. Two zoos reported having previously had unsuccessful mixed exhibits with capybaras and a male vicuña, which resulted in fighting and hunting of capybara offspring. Both zoos were only housing male maned wolves at the time.

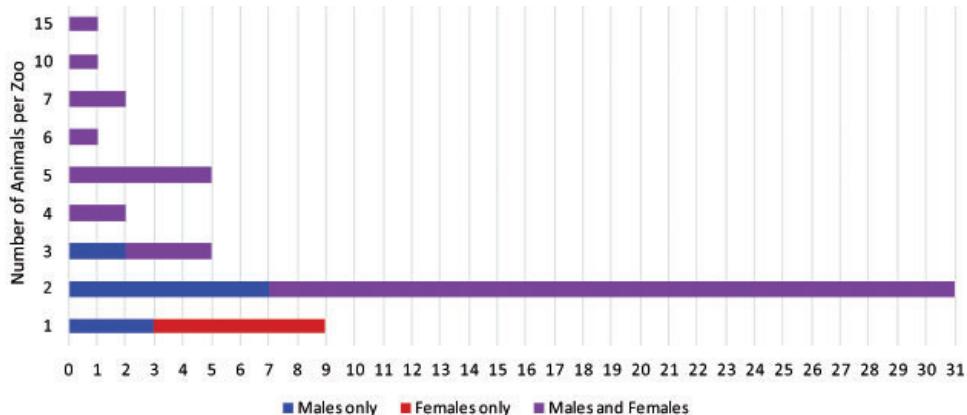


Fig. 5: Number of animals per zoo including differentiation between samesex and differentsex groupings.

The species most commonly housed next to the maned wolf enclosure were herbivores and birds (Fig. 6). 19 zoos (31%) reported that the maned wolves interacted with neighbouring species. Interactions included increased territorial marking in the direction of other canids, increased fighting among hyenas during the breeding season of the maned wolves, maned wolves chasing cheetahs along the fence, maned wolves hunting birds through the fence and species attentively observing each other and vocalising. Seven (30%) of the successful breeding pairs and three (20%) of the unsuccessful breeding pairs had interactions with neighbouring species.

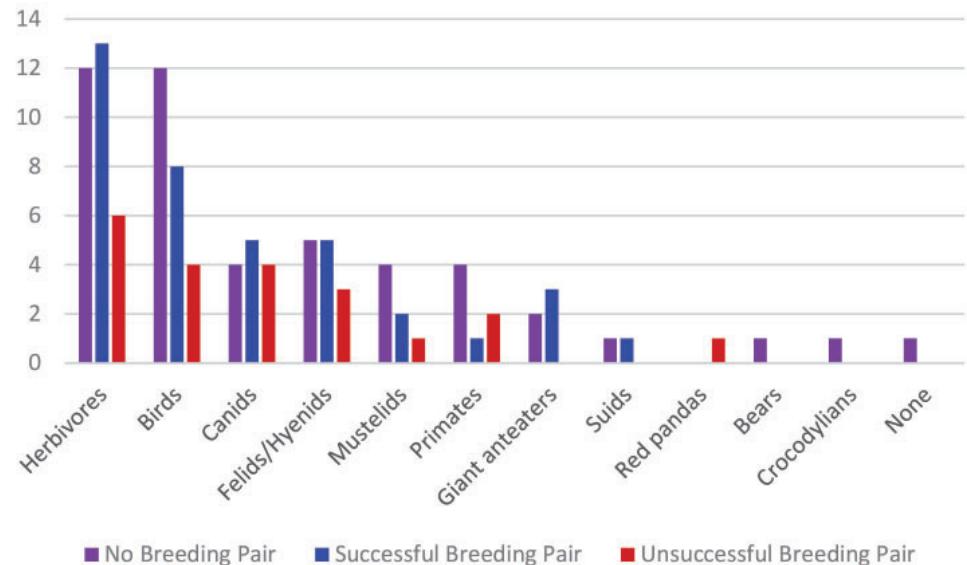


Fig. 6: Species housed next to maned wolves ranked by number of zoos in which they were the closest neighbouring species.

Zoo guests were allowed to bring dogs in 15 zoos (24%), ten of which (67%) reported interactions between dogs and maned wolves. Nine (60%) of the zoos that allowed dogs did not have a breeding pair, five (33%) had successful breeding pairs and one (7%) had an unsuccessful breeding pair. Interactions included maned wolves barking and growling or both parties displaying playful behaviour.

Handling, Behaviour and Enrichment

29 (63%) zoos handled their maned wolves in direct contact and 17 (37%) in protected (indirect) contact (Table 2). 11 (65%) zoos with recent offspring and six (60%) zoos without recent offspring handled their maned wolves in direct contact. 23 (49%) zoos trained at least one command with their maned wolves. Nine (50%) zoos with recent offspring and two (22%) zoos without recent offspring trained their maned wolves. Commands trained included target training, weighing, presenting the mouth, encounters with visitors, applying external ectoparasite treatment in the form of a spot-on, and health checks.

Stereotypic behaviours reported in this study were pacing, which was defined as a maned wolf walking backwards and forwards on an unchanging path for at least five minutes, and fly-catching, which was reported as biting the air without any stimulus or explanation visible to keepers. Stereotypic behaviour was reported by seven (29%) of the total zoos, four (44%) zoos with recent offspring and none (0%) of the zoos without recent offspring.

The most common form of enrichment used across all facilities was having plants in the enclosure, which was used in all (100%) zoos (Table 2). 24 (86%) zoos reported that the maned wolves consumed plants growing in their enclosure, 22 (92%) of which reported the consumption of grass (Table 3). 14 (29%) zoos had water features in the maned wolf enclosure (Table 2), with a number of other zoos citing this as a desired feature. Six (11%) of the total zoos, three (16%) zoos with recent offspring and none (0%) of the zoos without recent offspring, offered piles of sand, dirt or leaves in the enclosure in order to promote hunting behaviour. Four (67%) of the six zoos visited during this study reported that their maned wolves hunted and killed wild animals that entered their enclosure. The most common enrichment methods used during feeding were whole animals (98%), fillable balls (57%), ice blocks (56%), fish (51%) and large bones (50%). The most popular enrichment methods that were unrelated to feeding or the structure of the enclosure were the use of herbs (74%) and bringing in excreta from other species (56%) as an olfactory stimulant. No relevant differences were evident between institutions with breeding pairs with or without recent offspring.

Nutrition and Feeding Management

Two (3%) of the 62 zoos fed an entirely meat-based diet consisting of only whole prey without any fruit or vegetables, while one (2%) zoo fed only Mazuri® Maned Wolf Diet supplemented with whole prey and meat (Table 3). The other 58 zoos (94%) fed an omnivorous diet, all of which (100%) included fruit and 40 (69%) of which included either raw and/or cooked vegetables. The most commonly fed fruit was banana, fed by 46 (82%) of the zoos that gave detailed information on the diet fed to their maned wolves, followed by apples, which were fed by 40 (71%) of these zoos. 38 zoos (61%) reported good acceptance of fruit and vegetables by their maned wolves, 7 (11%) reported poor acceptance and 17 (27%) did not comment on how well fruit and vegetables were accepted. Only one (2%) zoo reported actively feeding grass, wild sunflower and corn stalks as an additional source of fibre.

All but one zoo (98%) fed whole animals and 45 zoos (73%) fed either raw and/or cooked meat. The most common whole prey items were rats, which were fed by 52 (96%) of the zoos that gave

Tab. 2: Parameters surveyed concerning handling, behaviour and enrichment analysed for all facilities, facilities with breeding pairs with recent offspring (between 2017-2021) and facilities with breeding pairs without recent offspring (between 2017-2021).

	All facilities	Facilities with breeding pairs with recent offspring	Facilities with breeding pairs without recent offspring
Direct Handling	29 (of 46; 63%)	11 (of 17; 65%)	6 (of 10; 60%)
Indirect Handling	17 (of 46; 37%)	6 (of 17; 35%)	4 (of 10; 40%)
Training	23 (of 47; 49%)	9 (of 18; 50%)	2 (of 9; 22%)
Stereotypic Behaviour	7 (of 24; 29%)	4 (of 9; 44%)	0 (of 3; 0%)
Enrichment in Enclosure			
Varied Terrain	32 (of 53; 60%)	13 (of 18; 72%)	5 (of 12; 42%)
Plants	55 (of 55; 100%)	19 (of 19; 100%)	13 (of 13; 100%)
Water Features	14 (of 48; 29%)	5 (of 18; 28%)	1 (of 8; 13%)
Objects	49 (of 53; 92%)	17 (of 18; 94%)	11 (of 13; 85%)
Piles of Sand, Dirt, Leaves	6 (of 55; 11%)	3 (of 19; 16%)	0 (of 13; 0%)
Enrichment during Feeding			
Bones	25 (of 50; 50%)	8 (of 17; 47%)	5 (of 11; 45%)
Fish	25 (of 49; 51%)	12 (of 19; 63%)	3 (of 10; 30%)
Rawhide	6 (of 43; 14%)	0 (of 16; 0%) ^a	2 (of 8; 25%) ^b
Crickets	18 (of 46; 39%)	6 (of 18; 33%)	3 (of 8; 38%)
Whole Animals	61 (of 62; 98%)	23 (of 23; 100%)	14 (of 15; 93%)
Coconuts	3 (of 44; 7%)	0 (of 16; 0%)	0 (of 8; 0%)
Ice Blocks	25 (of 45; 56%)	12 (of 17; 71%)	5 (of 9; 56%)
Prey Simulation	6 (of 43; 14%)	4 (of 16; 25%)	0 (of 8; 0%)
Fillable Balls	26 (of 46; 57%)	11 (of 17; 65%)	6 (of 9; 67%)
Olfactory Stimulants and Toys			
Non-Fillable Balls	16 (of 43; 37%)	6 (of 16; 38%)	3 (of 8; 38%)
Filled PVC Pipes	13 (of 43; 30%)	5 (of 16; 31%)	2 (of 8; 25%)
Filled Cardboard Boxes	15 (of 50; 30%)	8 (of 18; 44%)	3 (of 10; 30%)
Sacks	10 (of 50; 20%)	4 (of 18; 22%)	2 (of 10; 20%)
Feathers	19 (of 43; 44%)	7 (of 16; 44%)	2 (of 8; 25%)
Herbs	34 (of 46; 74%)	14 (of 16; 88%)	6 (of 9; 67%)
Excreta from Other Species	24 (of 43; 56%)	11 (of 16; 69%)	4 (of 8; 50%)
Perfume	18 (of 46; 39%)	7 (of 16; 44%)	3 (of 9; 33%)
Commercial Lures	3 (of 43; 7%)	2 (of 16; 13%)	0 (of 8; 0%)
Other Species in Enclosure (for any period of time)	7 (of 49; 14%)	3 (of 18; 17%)	2 (of 10; 20%)

^{a-b} Percentages with different superscript letters differ significantly ($p<0.05$) for successful and unsuccessful breeding pairs for the given parameter (chi-square test).

detailed information on the diet fed to their maned wolves. 15 zoos (24%) fed Mazuri® Maned Wolf Diet and 23 zoos (37%) fed a variety of dry dog foods. 3 zoos (5%) fed both Mazuri® Maned Wolf Diet and dry dog food. No zoo (0%) fed exclusively Mazuri® Maned Wolf Diet and only one zoo (2%) fed Mazuri® Maned Wolf Diet as the only source of protein. The only diet items that differed statistically between facilities with breeding pairs with and without recent offspring were less frequent use of dry dog food, eggs and bamboo in those without recent offspring (Table 3).

Anecdotally, keepers observed food caching behaviour by maned wolves, in particular during whelping and pup rearing. Only small prey animals were used for caching but not dry foods, fruits or vegetables.

Health and Veterinary Management

The most commonly reported health concern within the past 15 years was poor body condition, which was reported by 14 zoos (23%) in total (Table 4). None of the reported health issues

Tab. 3: Parameters surveyed concerning nutrition, including how many facilities fed each food group, the voluntary consumption of plants growing in the enclosure and the acceptance of fruit and vegetables offered to the maned wolves.

		All facilities	Facilities with breeding pairs with recent offspring	Facilities with breeding pairs without recent offspring
Raw Meat		44 (of 62; 71%)	16 (of 23; 70%)	9 (of 15; 60%)
Cooked Meat		6 (of 62; 10%)	4 (of 23; 17%)	0 (of 15; 0%)
Whole Animals		61 (of 62; 98%)	23 (of 23; 100%)	14 (of 15; 93%)
Rats		52 (of 54; 96%)	20 (of 21; 95%)	11 (of 12; 92%)
Mice		26 (of 54; 48%)	9 (of 21; 43%)	4 (of 12; 33%)
Rabbits		29 (of 54; 54%)	11 (of 21; 52%)	5 (of 12; 42%)
Guinea Pigs		21 (of 54; 39%)	8 (of 21; 38%)	4 (of 12; 33%)
Chicks		27 (of 54; 50%)	10 (of 21; 48%)	4 (of 12; 33%)
Chickens		22 (of 54; 41%)	6 (of 21; 29%)	5 (of 12; 42%)
Quails		13 (of 54; 24%)	7 (of 21; 33%)	3 (of 12; 25%)
Pigeons		6 (of 54; 11%)	3 (of 21; 14%)	0 (of 12; 0%)
Other		5 (of 54; 9%)	2 (of 21; 10%)	1 (of 12; 8%)
Fish		24 (of 62; 39%)	11 (of 23; 48%)	3 (of 15; 20%)
Dry Dog Food		23 (of 62; 37%)	13 (of 23; 57%) ^a	3 (of 15; 20%) ^b
Mazuri® Maned Wolf Diet		15 (of 62; 24%)	5 (of 23; 22%)	6 (of 15; 40%)
Eggs		26 (of 62; 42%)	14 (of 23; 61%) ^a	3 (of 15; 20%) ^b
Dairy Products		5 (of 62; 8%)	3 (of 23; 13%)	1 (of 15; 7%)
Raw Fruit		58 (of 62; 94%)	22 (of 23; 96%)	13 (of 15; 87%)
Apples		40 (of 53; 75%)	17 (of 22; 77%)	9 (of 12; 75%)
Pears		26 (of 53; 49%)	11 (of 22; 50%)	5 (of 12; 42%)
Grapes		20 (of 53; 38%)	11 (of 22; 50%)	4 (of 12; 33%)
Bananas		46 (of 53; 87%)	21 (of 22; 95%)	9 (of 12; 75%)
Melons		20 (of 53; 38%)	11 (of 22; 50%)	4 (of 12; 33%)
Tomatoes		13 (of 53; 25%)	4 (of 22; 18%)	2 (of 12; 17%)
Avocado		10 (of 53; 19%)	3 (of 22; 14%)	3 (of 12; 25%)
Other		35 (of 53; 66%)	14 (of 22; 64%)	7 (of 12; 58%)
Raw Vegetables		33 (of 62; 53%)	14 (of 23; 61%)	7 (of 15; 47%)
Cooked Vegetables		18 (of 62; 29%)	9 (of 23; 39%)	2 (of 15; 13%)
Potatoes		12 (of 54; 22%)	4 (of 20; 20%)	2 (of 13; 15%)
Sweet Potatoes		12 (of 54; 22%)	4 (of 20; 20%)	2 (of 13; 15%)
Carrots		23 (of 54; 43%)	11 (of 20; 55%)	5 (of 13; 38%)
Other		18 (of 54; 33%)	7 (of 20; 35%)	4 (of 13; 31%)
Rice		17 (of 62; 27%)	6 (of 23; 26%)	4 (of 15; 27%)
Other (i.e. Honey, Porridge, Dried Fruit)		11 (of 62; 18%)	4 (of 23; 17%)	3 (of 15; 20%)
Supplements		43 (of 62; 69%)	17 (of 23; 74%)	11 (of 15; 73%)
Plants (i.e. Grass, Wild Sunflower)		1 (of 62; 2%)	1 (of 23; 4%)	0 (of 15; 0%)
Plants Consumed in Enclosure		24 (of 28; 86%)	10 (of 11; 91%)	5 (of 7; 71%)
Grass		22 (of 28; 79%)	9 (of 11; 82%)	5 (of 7; 71%)
Bamboo		6 (of 28; 21%)	5 (of 11; 45%) ^a	0 (of 7; 0%) ^b
Other		5 (of 28; 18%)	2 (of 11; 18%)	2 (of 7; 29%)
Acceptance of Fruit and Vegetables				
Good		38 (of 62; 61%)	14 (of 23; 61%)	8 (of 15; 53%)
Poor		7 (of 62; 11%)	3 (of 23; 13%)	1 (of 15; 7%)
Unknown		17 (of 62; 27%)	6 (of 23; 26%)	6 (of 15; 40%)

^{a-b} Percentages with different superscript letters differ significantly ($p<0.05$) for successful and unsuccessful breeding pairs for the given parameter (chi-square test).

differed significantly between zoos with successful and unsuccessful breeding pairs (Table 4). Staff at 24 (69%) zoos believed developing an objective body condition score for maned wolves was important. The average weight of all female and male maned wolves (aged 6 months to 15 years) in this study was 25.7 kg and 27.4 kg respectively. The average weight of maned wolves

Tab. 4: Symptoms of possible underlying diseases and diseases that occurred in facilities within the past 15 years, according to responses to the surveys and post-mortem reports. Diseases that only occurred in one or two facilities were not included in the table below. Poor body condition was judged subjectively or by using body condition scoring systems for dogs or cheetahs. No significant differences ($p<0.05$) were found for any of these parameters.

	All facilities (n = 62)	Facilities with breeding pairs with recent offspring (n = 23)	Facilities with breeding pairs without recent offspring (n = 15)
Poor Body Condition	14 (23%)	9 (39%)	5 (33%)
Cystinuria	13 (21%)	4 (17%)	2 (13%)
Nephritis	12 (19%)	5 (22%)	1 (7%)
Dermatitis	11 (18%)	6 (26%)	2 (13%)
Trauma	11 (18%)	5 (22%)	3 (20%)
Inflammatory Bowel Disease	9 (15%)	4 (17%)	2 (13%)
Neoplasia	8 (13%)	5 (22%)	0 (0%)
Cardiopathies	8 (13%)	3 (13%)	1 (7%)
Diarrhoea	6 (10%)	5 (22%)	0 (0%)
Hepatopathies	5 (8%)	2 (9%)	1 (7%)
Gastritis	5 (8%)	1 (4%)	0 (0%)
Enteritis	5 (8%)	0 (0%)	2 (13%)
Conjunctivitis	3 (5%)	2 (9%)	0 (0%)
Ectoparasites	21 (of 43; 49%)	11 (of 16; 69%)	4 (of 8; 50%)
Ticks	11 (of 43; 26%)	8 (of 16; 50%)	1 (of 8; 13%)
Fleas	8 (of 43; 19%)	3 (of 16; 19%)	2 (of 8; 25%)
Ear Mites	5 (of 43; 12%)	2 (of 16; 13%)	2 (of 8; 25%)
Mites	3 (of 43; 7%)	1 (of 16; 6%)	1 (of 8; 13%)
Flies	3 (of 43; 7%)	1 (of 16; 6%)	0 (of 8; 0%)

within the optimal age range for breeding (>3 to <8 years of age) was 25 kg for female maned wolves (18.7 kg – 34.2 kg) and 28.5 kg for males (19.2 kg – 37.5 kg). The five most common health concerns for all facilities were poor body condition (23%), cystinuria (21%), nephritis (19%), dermatitis (18%) and trauma (18%). Ectoparasites were reported by 21 (49%) of 43 facilities that gave more specific information on the health of their maned wolves.

39 (95%) of the zoos that gave information on preventative and prophylactic measures reported carrying out faecal exams to monitor parasitic diseases (Table 5). 21 (51%) of these zoos carried out prophylactic deworming and 12 (29%) used ectoparasite prophylaxis. Eight (50%) of the zoos with successful breeding pairs carried out prophylactic deworming and eight (50%) zoos also used ectoparasite prophylaxis. Of the facilities with unsuccessful breeding pairs, six (75%) carried out prophylactic deworming and one (13%) used ectoparasite prophylaxis. 26 (63%) zoos vaccinated their maned wolves against at least one viral disease, meaning 15 (37%) zoos never vaccinated their maned wolves. 12 (75%) of the zoos with successful breeding pairs carried out vaccinations, whereas only three (38%) of the zoos with unsuccessful breeding pairs vaccinated their animals; this difference was significant for the parvovirus vaccination (Table 5).

Reproductive Management

Of the 38 zoos that had a breeding pair at the time of the survey, 23 (61%) were classified as breeding pairs with recent offspring (between 2017-2021) and 15 (39%) were classified as breeding pairs without recent offspring (between 2017-2021). Of the 23 zoos with breeding pairs that produced offspring, four (17%) did not have offspring that survived to the age of one year or older.

Tab. 5: Preventative and prophylactic measures used by facilities in the care of their maned wolves (data from North America were not available for these parameters).

	All facilities (n = 41)	Facilities with breeding pairs with recent offspring (n = 16)	Facilities with breeding pairs without recent offspring (n = 8)
Faecal exams	39 (95%)	15 (94%)	7 (88%)
Testing for Heartworm	6 (15%)	2 (13%)	1 (13%)
Preventative Deworming	21 (51%)	8 (50%)	6 (75%)
Ectoparasite Preventatives	12 (29%)	8 (50%)	1 (13%)
Vaccinations	26 (63%)	14 (88%)	3 (38%)
Canine Distemper	23 (56%)	12 (75%)	3 (38%)
Parvovirosis	23 (56%)	13 (81%) ^a	3 (38%) ^b
Rabies	15 (37%)	6 (38%)	3 (38%)
Leptospirosis	18 (44%)	8 (50%)	3 (38%)
Lyme Disease	1 (2%)	1 (6%)	0 (0%)
Parainfluenza	11 (27%)	5 (31%)	2 (25%)
CAV-1	17 (41%)	9 (56%)	2 (25%)
CAV-2	2 (5%)	1 (6%)	0 (0%)
Vaccination Frequency			
Never	15 (37%)	2 (13%)	5 (63%)
Annually	14 (34%)	4 (25%)	2 (25%)
Bi-annually	2 (5%)	2 (13%)	0 (0%)
Irregularly	7 (17%)	5 (31%)	1 (13%)

^{a,b} Percentages with different superscript letters differ significantly ($p<0.05$) for successful and unsuccessful breeding pairs for the given parameter (chi-square test).

43 (69%) zoos gave information on whether or not they had used contraceptive measures in their maned wolves, either at the time of the survey or in the past (Table 6). 13 (30%) zoos had used at least one form of contraception, including six (38%) of the zoos with successful breeding pairs and three (38%) of the zoos with unsuccessful breeding pairs. Five (of 13; 38% or of 43; 12%) zoos used GnRH implants in their male maned wolves, three (60%) of which produced offspring anyway. All other forms of contraception were successful. They were castration, sterilisation, ovariohysterectomy and GnRH implants in females.

Six (10%) zoos did not have a breeding pair at the time of survey, but reported on their latest breeding pair and are therefore included in the following calculations for all zoos, but not in calculations for zoos with or without recent offspring. 24 (86%) breeding pairs were housed together at all times, four (14%) were separated at night and one (4%) zoo with multiple breeding pairs used three different housing constellations, which were breeding pairs always being housed together, only housed together during breeding season and only housed together during oestrus. 13 (87%) successful breeding pairs were housed together at all times and two (13%) were separated at night. All seven (100%) unsuccessful breeding pairs were housed together at all times (Table 6).

Gravidity was most commonly confirmed by observed copulation (73%) and visually observed increase in abdomen size (59%) in all facilities, as well as in facilities with recent offspring (60% and 67% respectively) and facilities without recent offspring (100% and 75% respectively). The dam's diet was changed during gravidity in five (25%) facilities, three (20%) facilities with recent offspring and two (67%) facilities without recent offspring. Changes in keeper routine were also made in five (24%) facilities, three (20%) facilities with recent offspring and one (50%) facility without recent offspring (Table 6). These changes included less movement of keepers in the enclosure, restricted access to the enclosure in the weeks before whelping and reduction of disturbing activities around the enclosure, such as driving by with loud vehicles or carrying out any form of maintenance in the area.

For whelping, four (27%) zoos with recent offspring and none (0%) of the zoos without recent offspring separated the dam and sire (Table 6). A specific whelping pen was available for the

Tab. 6: Parameters surveyed concerning reproduction and reproductive management analysed for all facilities that provided information on past or present breeding pairs, facilities with breeding pairs with recent offspring (between 2017-2021) and facilities with breeding pairs without recent offspring (between 2017-2021).

	All facilities that gave information on past or present breeding pairs	Facilities with breeding pairs with recent offspring	Facilities with breeding pairs without recent offspring
Use of contraception ...	13 (of 43; 30%)	6 (of 16; 38%)	3 (of 8; 38%)
... successfully	10 (of 13; 77%)	3 (of 6; 50%)	3 (of 3; 100%)
Housing of Breeding Pair	n = 28	n = 15	n = 7
Always Together	24 (86%)	13 (87%)	7 (100%)
Separated at Night	4 (14%)	2 (13%)	0 (0%)
Together during Breeding Season Only	1 (4%)	1 (7%)	0 (0%)
Together during Oestrus Only	1 (4%)	1 (7%)	0 (0%)
Gravidity			
Confirmation of Gravidity	n = 22	n = 15	n = 4
Observed Copulation	16 (73%)	9 (60%)	4 (100%)
X-Ray	1 (5%)	1 (7%)	0 (0%)
Visual Increase in Abdomen Size	13 (59%)	10 (67%)	3 (75%)
The Birth Itself	2 (9%)	2 (13%)	0 (0%)
Diet Changes	5 (of 20; 25%)	3 (of 15; 20%)	2 (of 3; 67%)
Behaviour Changes Dam	8 (of 19; 42%)	7 (of 15; 47%)	1 (of 2; 50%)
Changes in Keeper Routine	5 (of 21; 24%)	3 (of 15; 20%)	1 (of 2; 50%)
Whelping			
Separation of Dam and Sire	5 (of 21; 24%)	4 (of 15; 27%)	0 (of 2; 0%)
Fence Contact if No Reintroduction	2 (of 2; 100%)	2 (of 2; 100%)	N/A
Corralled in Familiar Enclosure	2 (of 19; 11%)	2 (of 15; 13%)	0 (of 2; 0%)
Corralled in Unfamiliar Enclosure	2 (of 19; 11%)	2 (of 15; 13%)	0 (of 2; 0%)
Specific Whelping Pen Available	10 (of 20; 50%)	7 (of 15; 47%)	1 (of 2; 50%)
Bedding in Whelping Area	12 (of 13; 92%)	10 (of 11; 91%)	1 (of 1; 100%)
Heat Source in Whelping Area	12 (of 14; 86%)	9 (of 11; 82%)	2 (of 2; 100%)
Light Source in Whelping Area	10 (of 14; 71%)	8 (of 11; 73%)	2 (of 2; 100%)
Temperature Monitoring in Whelping Area	8 (of 14; 57%)	6 (of 11; 55%)	2 (of 2; 100%)
Humidity Monitoring in Whelping Area	1 (of 14; 7%)	0 (of 11; 0%) ^a	1 (of 2; 50%) ^b
Whelping Box or Boxes	10 (of 17; 59%)	7 (of 13; 54%)	2 (of 2; 100%)
Whelping Observed	6 (of 19; 32%)	4 (of 15; 27%) ^a	2 (of 2; 100%) ^b
Lactation Period			
Sire Cleans Pups	5 (of 21; 24%)	4 (of 15; 27%)	1 (of 2; 50%)
Unknown	9 (of 21; 43%)	5 (of 15; 33%)	1 (of 2; 50%)
Sire Regurgitates for Pups	7 (of 21; 33%)	5 (of 15; 33%)	1 (of 2; 50%)
Unknown	11 (of 21; 52%)	7 (of 15; 47%)	1 (of 2; 50%)
Sire Carries Pups	3 (of 21; 14%)	1 (of 15; 7%) ^a	1 (of 2; 50%) ^b
Unknown	10 (of 21; 48%)	7 (of 15; 47%)	1 (of 2; 50%)
Diet Change - Increase	14 (of 19; 74%)	11 (of 14; 79%)	3 (of 3; 100%)
Behaviour Changes Dam	13 (of 18; 72%)	12 (of 14; 86%)	1 (of 2; 50%)
Changes in Keeper Routine	12 (of 20; 60%)	9 (of 14; 64%)	1 (of 2; 50%)
Number of Times Pups are Moved			
Never	7 (of 16; 44%)	4 (of 12; 33%)	1 (of 2; 50%)
Once	2 (of 16; 13%)	2 (of 12; 17%)	0 (of 2; 0%)
At Least Three Times	7 (of 16; 44%)	6 (of 12; 50%)	1 (of 2; 50%)
Access to Larger Enclosure (in weeks post-partum)	2 ± 4 (0-12; 15)	2 ± 4 (0-12; 13)	0 ± 0 (0; 2)
Access to Other Dens (in weeks post-partum)	2 ± 4 (0-12; 15)	2 ± 4 (0-12; 13)	0 ± 0 (0; 2)
Reasons for First Human Contact	n = 21	n = 16	n = 2
Sexing	19 (90%)	16 (100%)	2 (100%)
Weighing	15 (71%)	11 (69%)	2 (100%)
Vaccination	14 (67%)	11 (69%)	1 (50%)
Hand-rearing	1 (5%)	1 (6%)	0 (0%)
Chipping	14 (67%)	12 (75%)	1 (50%)

Tab. 6: Continued.

	Deworming	10 (48%)	7 (44%)	1 (50%)
	Age of First Human Contact (in weeks post-partum)	7 ± 6 (0-24; 16)	6 ± 3 (1-12; 14)	0 ± 0 (0; 1)
	Hand-Rearing Ever Done	5 (of 21; 24%)	4 (of 15; 27%)	0 (of 2; 0%)
	Reason for Hand-rearing	n = 5	n = 4	N/A
	Restless Behaviour	2 (40%)	1 (25%)	N/A
	Neglect	2 (40%)	1 (25%)	N/A
	Disappearance of a Pup	0 (0%)	0 (0%)	N/A
	Trauma of a Pup	2 (40%)	2 (50%)	N/A
	Death of a Pup	1 (20%)	1 (25%)	N/A
	Zoo Policy	0 (0%)	0 (0%)	N/A
	EEP/Breeding Programme Recommendation	1 (20%)	1 (25%)	N/A
	Other	2 (40%)	2 (50%)	N/A

^{a-b} Percentages with different superscript letters differ significantly ($p<0.05$) for successful and unsuccessful breeding pairs for the given parameter (chi-square test).

dam in seven (47%) zoos with recent offspring and one (50%) zoo without recent offspring. Seven (54%) of the zoos with recent offspring and two (100%) of the zoos without recent offspring had whelping boxes for the dam, regardless of if they had a specific whelping pen or not. Whelping was observed directly or via video monitors in four (27%) of the zoos with recent offspring and two (100%) of the zoos without recent offspring.

During the dam's lactation period, 11 (79%) zoos with recent offspring and three (100%) zoos without recent offspring changed the diet fed to the dam by increasing the total amount fed (Table 6). Nine (64%) zoos with recent offspring and one (50%) zoo without recent offspring changed the routine of their keepers during the lactation period in order to cause less disturbances to the dam and her pups. Of the zoos with recent offspring, four (27%) reported the sire participating in cleaning the pups, five (33%) reported the sire participating in regurgitating for the pups and one (7%) reported the sire participating in carrying the pups. Of the zoos without recent offspring, one (50%) reported the sire cleaning, regurgitating for and carrying the pups. In four (33%) zoos with recent offspring and one (50%) zoo without recent offspring, pups were never moved by their parents. In six (50%) zoos with recent offspring and one (50%) zoo without recent offspring, pups were moved at least three times.

The dam or pair was given access to a larger enclosure and additional dens on average two weeks after whelping in all facilities and facilities with recent offspring, and immediately after whelping in facilities without recent offspring (Table 6). The first human contact with the pups was at seven weeks after whelping on average, at six weeks after whelping in facilities with recent offspring and immediately after whelping in facilities without recent offspring. Five (24%) zoos reported having hand reared pups at some point, four (27%) of which were zoos with recent offspring and none (0%) of which were zoos without recent offspring.

Discussion

These results represent a comprehensive comparative analysis of maned wolf husbandry and management practices across European, North American and Australian zoological institutions. Evident limitations of the study apply, including the fact that not all facilities keeping maned wolves were responsive, that not all responsive facilities answered all questions, and that even though answers were most likely given to the best of the respondents' knowledge, these answers need not necessarily match actual conditions that would have been observed had actual visits

been feasible. Nevertheless, the results of this survey yield important information for maned wolf husbandry; in particular, they suggest that the reproductive management of the species is complex and not easily fixed by a few, readily detectable factors.

Factors Affecting Reproduction

This survey did not yield evidence for factors clearly associated with the low reproductive success of the current maned wolf population; therefore, we can only speculate on factors that might be relevant. A significant limitation to the statistical reliability of these results is that pups that are stillborn and/or immediately eaten by a parent or sibling are not always discovered or reported, therefore potentially skewing the findings. The first-year mortality of maned wolves has not improved over recent decades, most recently even increasing despite attempts to improve reproductive success in the species (Roller et al., 2021). In this study, of the 23 zoos with breeding pairs that produced recent offspring (between 2017–2021), four (17%) did not have offspring that survived to the age of one year or older. No significant differences were detected between these four zoos and the 19 zoos with surviving offspring; however, this is potentially due to the small sample size of zoos without surviving offspring and may warrant further research.

Stereotypic behaviours were not observed in unsuccessful breeding pairs, but in 44% of successful breeding pairs. Observations carried out during this study suggested that female maned wolves that were housed with previous offspring close to or during their next fertile period and potential gravidity were most likely to show signs of stereotypic behaviour. Anecdotal evidence from keepers suggested that previous offspring being present when a new litter was born frequently resulted in the litter being eaten by a parent or sibling. Rodden et al. (2007) states that most zoos separate pups from parents when the pups are close to ten months old, to prevent interference with the next breeding season. However, there appears to be some evidence from free-ranging populations suggesting female offspring may be involved in assisting in raising their mother's next litter (Rodden et al., 2007).

Paternal parenting behaviour has been described in maned wolves (Veado, 1997) and a higher rate of survival has been observed in pups raised by both parents, rather than just by the dam. Furthermore, female pups that were raised by both parents are more likely to successfully raise future litters of their own (Bestelmeyer, 2000). Dietz (1984) observed at least one free-ranging male maned wolf involved in the parental care of his pups, assuming that he was bringing food to the dam while she remained in the den with the pups. Anecdotal evidence from multiple keepers interviewed during this study indicated similar behaviours, stating that in the first weeks post-partum, the sire would bring food to the dam while she remained in her den. As soon as the pups were old enough to start eating small prey items, the sire would become more involved in supplying the pups with food and the dam would recommence feeding herself. These observations are also corroborated by Rodden et al. (2007). Therefore, the recommendation of housing pairs together year round was made in the 2007 Maned Wolf Husbandry Manual, which was done by all zoos with unsuccessful breeding pairs in this study and 87% of zoos with successful breeding pairs. Of the zoos with recent offspring, four (27%) reported the sire participating in cleaning the pups, five (33%) reported the sire participating in regurgitating for the pups and one (7%) reported the sire participating in carrying the pups. For each of these three questions, around 50% of zoos stated that they could not be sure whether or not the sire showed parental behaviours; therefore, paternal involvement is potentially much more frequent. All this evidence supports the recommendation to allow the sire to remain with the dam throughout all stages of reproduction and to monitor his paternal behaviours in order to aid future decisions for the breeding pair.

Rodden et al. (2007) states that video monitoring should be possible in nesting boxes offered to female maned wolves. In this study, whelping was observed directly or via video monitors in four (27%) of the zoos with recent offspring. Video monitoring could be a valuable tool for zoos with recently successful or unsuccessful breeding pairs, as video footage would improve observations of how many pups are born and lost in each litter, and of pairs that are potentially breeding but lose the entire litter before pups emerge from the den. In this study, zoos with unsuccessful breeding pairs (53%) locked their maned wolves out during the day significantly more than those with successful breeding pairs (22%). This could be an effect of zoos with unsuccessful breeding pairs having less animals for display. Nevertheless, not locking the maned wolves out from the beginning of the breeding season to the end of the normal whelping season should be attempted and evaluated as a potential mitigation of lost pregnancies or litters.

Brady & Ditton (1979) state that disturbing a dam with her pups will trigger an attempt to relocate her pups, and failure to do so will lead to the neglect or killing of the pups. Rodden et al. (2007) also recommends keeping disturbances directly after whelping to an absolute minimum, stating pups should ideally not be handled until they receive their first vaccinations at six to eight weeks. In our survey, there was a large variability in how many weeks post-partum pups had their first human contact, ranging from directly after whelping, in a zoo concerned about the dam not accepting the pups, to 24 weeks post-partum, in a zoo that did not routinely vaccinate pups. 67% of zoos vaccinated their pups at first human contact. In terms of other disturbances, 60% of zoos made changes to their keeper routine after whelping, including less movement of the keepers in the enclosure and reduction of disturbing or loud activities in the immediate vicinity of the enclosure.

In our study, a significantly higher vaccination rate against parvovirosis was found in zoos with successful breeding pairs (81%) than in those with unsuccessful breeding pairs (38%). Historically, there have been reports of adverse effects of parvovirus vaccination in maned wolf pups (Backues, 1994), as well as vaccination induced canine distemper (Thomas-Baker, 1985). These reports could be a potential reason why some zoos are hesitant to vaccinate their pups; however, vaccinating against these diseases is still recommended using Merial's PUREVAX® Ferret Distemper recombinant canary pox vector vaccine and killed feline parvo vaccines, to minimise the risk of vaccination reactions in pups (Rodden et al., 2007). As Parvovirosis in carnivores has been reported to cause foetal death and embryo resorption, it is especially advisable to vaccinate animals with low reproductive success (Steinel et al., 2001), and our findings support this concept.

Health Concerns Currently Relevant in the Population

In this study, the five most common health concerns occurring over the past 15 years across all facilities were poor body condition (23%), cystinuria (21%), nephritis (19%), dermatitis (18%) and trauma (18%). Observations carried out during this study and anecdotal evidence from keepers and curators suggested that poor body condition was most frequently observed in lactating dams. In the 2007 Maned Wolf Husbandry Manual, the average weight of adult males was 31 kg and that of females was 30 kg (Rodden et al., 2007), whereas in the current study the average weights of adult male and female maned wolves within the optimal breeding range (>3 years to <8 years) were 28.5 kg and 25 kg respectively. As there is, as of yet, no objective body condition scoring system available for maned wolves, it is difficult to discern whether the lower average weights are an indication of a move from optimal to poor body condition, or from animals being overweight to being in optimal condition. As 69% of zoos in this study believed the creation of an objective body condition scoring system to be important and poor body condition appears to be such a prevalent issue in the zoo-kept population, the creation of such an objective tool should be a priority for future management.

The high rates of cystinuria and nephritis reported by zoos in this study are unsurprising, considering the large amount of research already available discussing this issue (Bush & Bovee, 1978; Bovee et al., 1981; Boniface, 1998; Mussart & Coppo, 1999; Childs-Sanford, 2005; Childs-Sanford & Angel, 2006; de Oliveira & das Graças Mendes, 2007). A possible explanation for the high rates of cystinuria and nephritis is that the medical data evaluated within this study spans the past 15 years; however, the most extensive research on improved feeding of maned wolves to prevent cystinuria (Childs-Sanford, 2005; Childs-Sanford & Angel, 2006) was only published around 15 years ago. Therefore, the changes made to feeding practices would not have positively affected animals that were diagnosed with cystinuria and/or nephritis towards the beginning of these 15 years.

The issues of dermatitis and trauma warrant further investigation. Dermatitis could not be statistically linked to the presence of ectoparasites or the use of preventatives against ectoparasites. Therefore, investigations into other causes, such as excessive or stereotypic licking or irritating substances or plants in the environment should be considered.

The 2007 Maned Wolf Husbandry Manual suggests that at least semi-annual faecal exams, treatment against ectoparasites with canine dosages of domestic animal products when necessary, and testing and prophylaxis against heartworm in endemic areas should be part of the medical management of maned wolves (Rodden et al., 2007). In this study, 95% of zoos reported carrying out at least annual faecal exams, 15% of zoos tested for heartworm and 29% used ectoparasite preventative medication, even though 49% of zoos reported their maned wolves having had ectoparasites at least once. Possibly, intensifying ectoparasite surveillance could be advised for maned wolves.

Comparison of Previous and Current Feeding Practices to Natural Diets

According to Rodden et al. (2007), zoos outside North America were feeding small amounts of animal protein in 2007, the bulk of their diets consisting of rice and other grains, fruits and vegetables. The recommendation in the 2007 Maned Wolf Husbandry Manual was that at least 60-70% of the dry matter intake should be made up of nutritionally complete commercial products such as dry dog food, in order to prevent vitamin and mineral deficiencies. However, it was also noted that domestic dog diets containing soybean meal could lead to poorly formed stools and should therefore be avoided (Rodden et al., 2007).

As is illustrated in Figure 7, the proportion of food types fed varied greatly, even within zoos on the same continent. The most notable difference between diets fed in North American zoos in comparison to European and Australian zoos is that North American zoos fed an average of 46% commercial foods (dog foods, Mazuri® Maned Wolf Diet and the category 'Other' in Fig. 7), whereas European zoos fed only 8% commercial foods and the Australian zoo fed 7% commercial foods.

The most distinct differences between all of these diets and the diets of free-ranging maned wolves are the almost complete lack of grasses in the zoo diets, as well as a far lower proportion of invertebrates and the complete lack of *Solanum sp.* (Fig. 1 & Fig. 7). Only one zoo in this study actively fed grasses and other fibrous plants as a source of fibre and enrichment. 86% of zoos reported that their maned wolves consumed plants growing in the enclosure, thereby underlining the importance of making these plants available to the animals, potentially supplementing them with alternatives in winter, and selecting the plants, especially grasses, growing in the maned wolves' enclosure with particular care.

It is also noteworthy that in all 12 studies concerning the diets of free-ranging maned wolves considered in Fig. 1, the proportion of animal matter (including invertebrates) and plant matter consumed is consistently almost equal. As most of these studies used scat samples to make these

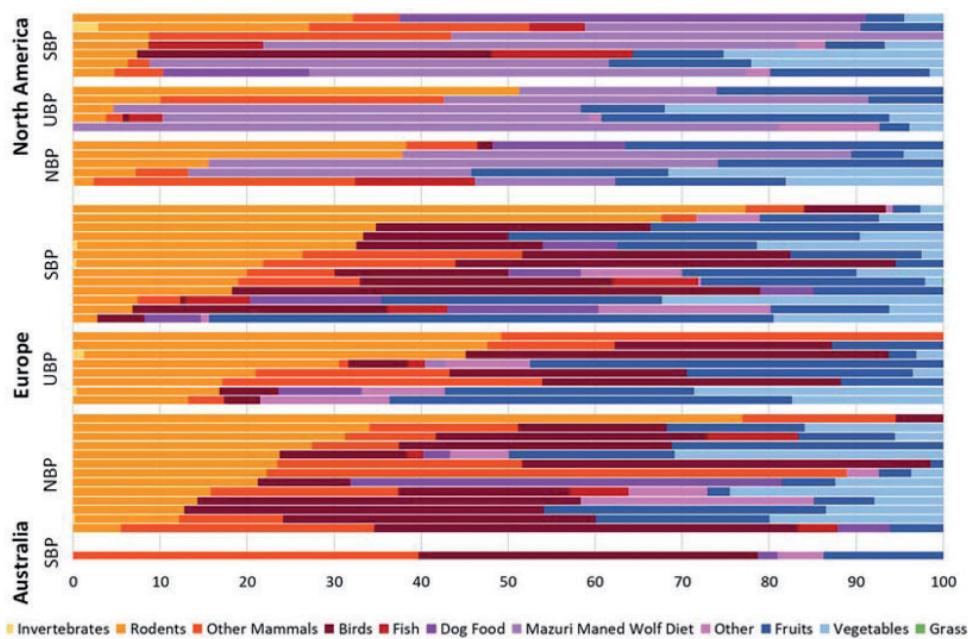


Fig. 7: Proportion of invertebrates, rodents, other mammals, birds, fish, fruits, vegetables, grass, dog food, Mazuri® Maned Wolf Diet and other foods in the diet of maned wolves kept in zoos in North America, Europe and Australia. (SBP = successful breeding pairs, UBP = unsuccessful breeding pairs, NBP = no breeding pairs).

analyses, it is important to note that plant matter and certain parts of invertebrates are less easily digestible than most vertebrates. It is therefore likely that the proportion of vertebrates consumed is somewhat higher than discernible in these studies. Bearing this in mind, there is still a strong contrast between these natural diets and the two (3%) zoos that fed an entirely meat-based diet consisting of only whole prey without supplementation of fruit, vegetables or grains and the one (2%) zoo that fed only Mazuri® Maned Wolf Diet supplemented with whole prey and meat. It is important to note that only 61% of zoos reported good acceptance of fruit and vegetables, 11% reported poor acceptance and 27% did not comment on acceptance. A general consensus of the keepers interviewed during this study was that maned wolves will always eat the meat or whole prey portion of their diet first, then the fruit portion, and vegetables are most often left over. Therefore, the total amount of meat or whole prey fed is essential in deciding whether the animals will still be hungry enough to eat fruits and vegetables afterwards. Bearing this in mind, the formulation of maned wolf diets should not only focus on the proportion of animal protein to fruits and vegetables, but also the total amount of these foods offered. Anecdotal evidence from keepers in some of the zoos visited during this study suggested that maned wolves responded with diarrhoea to the introduction of new fruit and vegetables, as well as the sporadic feeding of fish. The implication of this could be that novel fruits and vegetables should be tested for longer periods of time in order to discover whether the maned wolves' digestive system will grow accustomed to these foods or if there is a true intolerance.

As maned wolves show food caching behaviour similar to red foxes and other carnivores (Macdonald 1976), a diet made up of commercial foods that does not include any small prey items restricts this natural behaviour. Restricting food caching behaviour could have a negative

impact on the reproductive success of maned wolves, as this behaviour was most notably observed and reported during the whelping and pup rearing season in this study. Keepers reported sires bringing food to their dams in the weeks after whelping, which they would then eat or cache for a later time. A lack of food to cache during this critical period could contribute to motivations for infanticide or neglecting of the pups. Furthermore, when pups were old enough to begin eating small prey items themselves, some sires were observed both bringing these to their pups as well as caching them and digging them up for the next day. As the only foods reportedly cached by maned wolves were small prey animals, at least some portion of the diet should be made up of small prey items to allow for this behaviour. Possibly, increasing the amount of small prey during the lactation period could be beneficial for both behavioural and energetic reasons, and should be investigated in practice.

Conclusion

Unfortunately, the results of this study do not allow for any evidence-based recommendations. However, in order to address the poor reproductive success of the species, monitoring of the whelping den during whelping season could be a useful step to gather more information on the current situation as a whole, but also to enable zoos to gain a better understanding of their individual breeding pairs. It is also advisable to offer dams multiple den sites that are warm enough and freshly padded for the whelping season, in order to give options for the safe movement of pups in cold temperatures. Based on the observations made during this study, it is also recommended to remove previous offspring from the breeding pair at the time of the new breeding season and allow the sire to remain with the dam and pups, unless there are individual reasons that indicate this to be a poor choice for a specific breeding pair. In order to mirror natural diets more closely, zoo diets should aim to achieve a more equal balance of plant and animal material, especially focusing on supplying sources of fibre such as grasses and allowing for food caching behaviour by offering small prey animals, in particular during the whelping and lactation period. These dietary changes could yield positive results in the prevalence of cystinuria and nephritis, as well as poor body condition. Therefore, a regular re-evaluation of these medical concerns would be beneficial to verify a possible reduction in prevalence in the population. Additionally, in order to evaluate the issue of poor body condition more objectively, it would be valuable to prioritise creating an objective body condition scoring system for this species.

Acknowledgements

We thank all involved zoological institutions for their participation in this study.

Zusammenfassung

Die Mähnenwolf-Population *ex situ* weist historisch einen geringen Fortpflanzungserfolg und eine hohe Prävalenz von Cystinurie auf, was mit einer auf tierischen Bestandteilen basierten Fütterung dieser omnivoren Art zurückgeführt wurde. Eine Umfrage bei 62 europäischen, nordamerikanischen und australischen Zoos zu Haltung, Fütterung, Fortpflanzung und tiermedizinischer Betreuung sammelte Angaben zu 169 Tieren (81 weibliche, 86 männliche und 2 ohne Geschlechtsangabe) im Alter von einem Monat bis 16 Jahren. Diese Studie zeigt auf, dass das

paternale Elternverhalten, restriktiver Zugang zu Innengehegen, die Anwesenheit der Nachkommen des vorigen Jahres sowie lückenhaftes Monitoring wichtige Faktoren für den Fortpflanzungserfolg sein könnten. Die häufigsten für die letzten 15 Jahre genannten Gesundheitsprobleme waren schlechte Körperkondition, Cystinurie und Nierenentzündung. Die Fütterung variierte erheblich zwischen Zoos, wobei nordamerikanische Zoos typischerweise das Mazuri® Maned Wolf Komplettfutter einsetzen oder kommerzielles Hundefutter, während europäische und australische Zoos kleine Beutetiere mit unterschiedlichen Anteilen von Obst und Gemüse fütterten. Der wichtigste Unterschied aller Zoo-Rationen zur natürlichen Nahrung war ein Mangel an Gräsern und *Solanum*-Früchten. Die Ergebnisse legen nahe, dass Zoo-Rationen die natürliche Nahrung eher imitieren würden, wenn sie gleiche Anteile an tierischen und pflanzlichen Bestandteilen enthielten; dies könnte möglicherweise auch zur Behebung von schlechter Körperkondition und Cystinurie beitragen. Um den ausbleibenden Zuchterfolg nachhaltig zu beheben, sind gezielte Studien inklusive eines genauen Monitorings während der Jungtieraufzucht notwendig.

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DER ZOOLOGISCHE GARTEN

THE ZOOLOGICAL GARDEN

Volume 91
Issue 1 · 2023
ISSN 0044-5169

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