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Welfare in zoo kept felids

A study of resource usage

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Sammanfattning
Abstract

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Nyckelord
Keyword

Behaviour, Enclosure usage, Felids, Resources, Welfare, Zoo

Content

1 Abstract

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Keywords: Behaviour, Enclosure usage, Felids, Resources, Welfare, Zoo.

2 Introduction

According to IUCN Red List of Threatened Species (2014) 17 of 37 felid species are vulnerable or threatened of extinction in the wild, only four are not declining in number. On subspecies level even more are close to extinction (IUCN, 2014). Therefore there are ongoing conservation projects both *in situ* and *ex situ* with the aim of restoring and conserving populations of felids in the wild as well as maintaining functional gene pools in zoos (Henry *et al*. 2009).

Felids, members of the biological family *Felidae*, are all carnivorous animals with a similar morphology (Sunquist & Sunquist 2002). Felids have the widest range of body size of all *Carnivora* families, from the Rusty-spotted cat (*Prionailurus rubiginosus*) of about 0.9 kg to the massive 300 kg of the Amur tiger (*Panthera tigris altaica*) (Sunquist & Sunquist

2002). Although they live in a wide range of ecological niches, from cold barren mountainous areas to hot deserts or dense forests, they share many behavioural similarities, such as the way they move, kill their prey or live a more or less a solitary life with large home ranges and low density (Sunquist & Sunquist 2002). Therefore it is easy to rush to conclusions about their ethology without having the knowledge from research. Most felids are crepuscular and since they live wide apart and are able to move over vast areas, they are hard to study (Sunquist & Sunquist 2002). Thus we might miss much knowledge of the felids ethology.

Habitat loss, human expansions and conflicts between humans and felids are severe causes of decline in felids. In a review of felid-human conflicts Inskip & Zimmermann (2009) found that even if there are evidences of conflicts affecting as many as over 75 % of the felid species, there are gaps in knowledge. Although much effort is made to manage these conflicts, few conservation strategies are being scientifically evaluated. Inskip & Zimmermann (2009) also found an uneven distribution of knowledge among the different species and a bias in research towards large felids. They state that in order to work with conservation of felids these gaps of knowledge must be filled.

When there are severe conflicts with humans and no space left for the felids, conservation work *ex situ* is an important complement to conservation efforts *in situ*. Modern zoos have a responsibility to work with conservation projects (EAZA 2015). They need to inform visitors about threats and inspire others to work for preserving biodiversity and reduce the human footprint on the environment as well as keeping a healthy population of animals to support the wild ones. Threatened species are managed in breeding programmes controlled by the zoo organisations. In the European Association of Zoos and Aquaria (EAZA) there are two levels of breeding programs, the European Endangered species Programme (EEP) and the European StudBook (ESB) involving species from all over the world (EAZA 2015). Currently there are 18 EEPs and four ESBs with felids (EAZA 2015). The Association of Zoos and Aquariums (AZA) in the USA has 20 felids in its Species Survival Plan (SSP) (AZA 2014). The Australasian Species Management Program (ASMP) of the Zoo and Aquarium Association (ZAA) includes five felids (ZAA 2015). The World Association of Zoos and Aquariums (WAZA) includes three felids in its Global Species Management Plans (GSMPs) (WAZA 2015).

Wild animals kept in zoos are protected against starvation, predation and other risks and are therefore often healthier and breed more successfully than free living animals (Mason 2010). Even so there are some species, such as felids, with severe problems with for instance low fecundity, young mortality and stereotypic behaviours (Hope & Deem 2006, Mason 2010). Stereotypic behaviours, most typically pacing, are common in captive felids (Mason & Latham 2004).

Environmental enrichments are used to increase animal welfare and decrease or inhibit occurrence of stereotypic behaviours (Mason *et al*. 2007). In contrast to earlier beliefs that connected stereotypic behaviours with prohibited hunting behaviours, Clubb & Mason (2007) found that the frequencies of stereotypic behaviours in carnivores are strongly connected with natural ranging behaviour. The larger the home range and species-specific daily travel distances the more stereotypic behaviours and also higher infant mortality rates (Clubb & Mason 2007). Because space is an issue in many zoos it is hard to provide the wide ranging felids with enough enclosure space. Much environmental enrichment is therefore still associated with feeding and foraging or attempts to make the environment more complex by for instance odours (Skibiel *et al*. 2007, Quirke & O'Riordan 2011b, Resende *et al*. 2011).

Stereotypic behaviours are complex. They are probably a result of frustration or attempts to cope with a situation of poor welfare (Mason *et al*. 2007) but they may become fixed habits that remain even though the welfare issues have been resolved (Mason 2010). According to Mason *et al*. (2007) stereotypic behaviour can be the result of a dysfunction in the central nerve system as a result of suboptimal conditions impairing brain development. Stereotypic behaviour is theorized to be an attempt to cope with a stressful situation and it might even be that the animal with stereotypic behaviours has a better welfare or is better to cope with a suboptimal situation than the animal without stereotypic behaviour (Koolhaas *et al*. 1999, Mason 2010). Even though stereotypic behaviours might be a result of earlier experiences or a functional coping mechanism we need to consider it as a serious sign of suboptimal welfare (Mason 2010).

Low fecundity and breeding success in many felids are severe problems in the conservation work. For instance the cheetah (*Acinonyx jubatus*) population in Western zoos are not self-sustained because of reproductive problems and high infant mortality (Bauman *et al*. 2010) and many small felids in American zoos have propagation problems (Swanson 2006, Moreira *et al*. 2007). Unsuccessful breeding might be a result of long-term or chronic stress due to poor welfare. Increased corticoid production suppresses ovarian follicular activity and disturbs the reproductive cycle (Moreira *et al*. 2007). It is common to hold cheetahs in pairs or groups but Wielebnowski *et al*. (2002) found that keeping female cheetahs in pairs might lead to suppressed ovarian cyclicity.

It is a common view that felids need large space, multiple den sites and resting places, environmental complexity and variability, and more control over their situation (Clubb & Mason 2007, Morgan & Tromborg 2007, Fanson & Wielebnowski 2013). I would like to challenge this view and ask if this is founded in scientific research or old beliefs. Do all felid species have the same needs and is there an order of priority in availability of resources?

2.1 Aims

To successfully manage wild felids in zoos with an optimal welfare we need to have more knowledge about which resources are most important for the welfare and how these needs differ among the different felid species.

The first aim of this study was to review the literature on welfare in zoo kept felids in order to map out the state of knowledge about felid welfare, their needs, and if these needs differ between species of felids.

The second aim was to examine the practiced husbandry of felids in zoos and compare this to the scientific findings in order to highlight gaps in knowledge and see if anecdotal and scientific knowledge collides.

The third aim of this study was to do a behavioural study of enclosure usage and use of resources in the enclosures in seven species of felids; Amur tiger (*Panthera tigris altaica*), Sumatran tiger (*Panthera tigris sumatrae*), Amur leopard (*Panthera pardus orientalis*), Persian leopard (*Panthera pardus saxicolor*), Snow leopard (*Uncia uncia*), Cheetah (*Acinonyx jubatus*) and Pallas's cat (*Otocolobus manul*), and try to find an order of priority in availability of resources.

The hypothesis for the behavioural study was that even though behaviours might be similar in all felid species, the use of, and need for, certain resources probably differ between species. Several other factors and individual preferences are likely also important in the choice of resources why it might not be possible to distinguish a general priority of resources.

3 Material & methods

3.1 Literature review

Scientific literature about welfare in captive felids with the focus on behaviour was reviewed. Articles were searched for in the databases Web of Science and Scopus with the search strings “felid” OR “feline” OR “cat” AND “welfare” AND “zoo” OR “captivity”; “felid” OR “feline” OR “cat” AND “behaviour” AND “zoo” OR “captivity”.

All research articles published between and including the years 2005-2015 were analysed and categorized according to subject and method used in the studies. Data from the articles were categorised and compiled to get an overview of research coverage.

3.2 Examination of practiced husbandry

For the study of practiced husbandry seven species of felids were selected; Amur tiger (*Panthera tigris altaica*), Sumatran tiger (*Panthera tigris sumatrae*), Amur leopard (*Panthera pardus orientalis*), Persian leopard (*Panthera pardus saxicolor*), Snow leopard (*Uncia uncia*), Cheetah (*Acinonyx jubatus*) and Pallas’s cat (*Otocolobus manul*).

In order to maintain successful breeding programs in EAZA, husbandry guidelines are used as manuals for the holding and care of the specific species within the breeding program. These guidelines are general for the whole EAZA community and do not take into account any national legislations.

For the selected seven species of felids four husbandry guidelines are used by EAZA members; Husbandry Manual for the Cheetah *Acinonyx jubatus* (Ziegler-Meeks 2009), EAZA Leopards *Panthera pardus spp.* Husbandry Guidelines (Houssaye & Budd 2009), Pallas's cat EEP Husbandry Guidelines (*Otocolobus manul*) (Barclay 2013) and EEP-Husbandry Recommendations for Tigers (*Panthera tigris*) (Richardson & Lewis 2010).

These four EAZA husbandry guidelines were examined and the data compiled and compared to the reviewed articles.

3.3 Behavioural observations

Behavioural studies were performed in four Swedish zoos; Borås Zoo, Nordens Ark, Orsa rovdjurspark and Parken Zoo, between August 4 and October 4 2015.

The same seven species of felids as for the study of husbandry practice were selected for the behavioural studies; Amur tiger (*Panthera tigris altaica*), Sumatran tiger (*Panthera tigris sumatrae*), Amur leopard (*Panthera pardus orientalis*), Persian leopard (*Panthera pardus saxicolor*), Snow leopard (*Uncia uncia*), Cheetah (*Acinonyx jubatus*) and Pallas's cat (*Otocolobus manul*).

3.3.1 Animals

In total seven Amur tigers, four Sumatran tigers, five Amur leopards, four Persian leopards, five snow leopards, five cheetahs and four Pallas's cats were observed (Table 1). All animals were observed in their normal enclosures.

At Borås Zoo the two Amur tigers were outside in one exhibit enclosure 24 hours per day except for short periods when they were let inside to enable keepers to clean the exhibit or put in food. Three out of five adult cheetahs in the zoo were included in the study. The cheetahs were rotated between one large exhibit enclosure and several small back enclosures. During the observation period the female with cubs was only observed in the exhibit enclosure where they were from approximately 09.00 to 16.00 every day. The two males were held in two connected back enclosures. The males were let out in the exhibit enclosure during most nights (approximately 16.00 to 08.00) and were therefore observed in the exhibit enclosure in the last session during two days of the observation period.

At Nordens Ark all animals were in their exhibit enclosures 24 hours per day. The Amur tigers were rotated between two large exhibit enclosures (called Large and Medium in the study) and a small exhibit enclosure connected to an indoor area and a small back enclosure (called Small in the study). All three enclosures are connected with two cage locks and these cage locks were always open to one of the enclosures but it varied to which one. The Pallas's cats and Amur leopards were held in separate enclosures for each individual; the female Pallas's cat was kept together with her four kittens. The Persian and snow leopards were held together with their conspecifics in three connected enclosures for each species.

At Orsa rovdjurspark the animals were in exhibit enclosures during opening hours, 10.00 to 15.00, each day. When the park closed they were let indoors and were fed there. The leopards had the opportunity to go out again if they chose. The tigers were held in the back and indoor enclosures between 15.30 and 08.00. During the days the female Persian leopard and female snow leopard had access to the inside area including the parts where their respective conspecific males were during the nights.

At Parken Zoo the female Amur leopards had access to an indoor area all the time except during two sessions where they were locked out. The male Amur leopard was outside in his enclosure 24 hours per day. The Pallas's cats had constant access to an indoor area and also to a hut inside a large cairn in the enclosure but were kept in the enclosure 24 hours per day. The Pallas's cats were confirmed to have a kitten shortly after the observation period ended. The Sumatran tigers were in their enclosure all the time except for short periods when the enclosure was cleaned or keepers put in food. The cheetahs were kept inside during the nights and let out at approximately 8 in the mornings.

Table 1. Overview of behavioural observations in four zoos, Borås Zoo (BZ), Nordens Ark (NA), Orsa Rovdjurspark (OR), Parken Zoo (PZ). The animals are listed as number of "males, females, offspring". They were held either individually, in social groups or as female with her offspring.
**Individuals were rotating between the enclosures. ** Indoor enclosure size for the animals kept indoors during the nights.*

Obs. period	*No of days*	*Zoo*	*Species*	*No of sessions*	*Minutes observed*	*Animals*	*Born (y)*	*Social context*	*Enclosure size (sq.m.)*
1	6	NA	Amur leopard, *P. pardus orientalis*	18	540	1,0	2009	Individual	670
1	6	NA	Amur leopard, *P. pardus orientalis*	18	540	0,1	2009	Individual	540
1	6	NA	Pallas's cat, *O. manul*	18	540	1,0	2009	Individual	300
1	6	NA	Pallas's cat, *O. manul*	18	540	0,1,4	2010, 2015	Female with kittens	300
2	6	PZ	Amur leopard, *P. pardus orientalis*	18	540	1,0	2007	Individual	800
2	6	PZ	Amur leopard, *P. pardus orientalis*	18	540	0,2	2010, 2014	Social	550
2	6	PZ	Pallas's cat, *O. manul*	36	1080	1,1	2007, 2014	Social	390
3	6	PZ	Cheetah, *A. jubatus*	36	1080	1,1	2006, 2008	Social	3080 **82
3	6	PZ	Sumatran tiger, *P. tigris sumatrae*	36	1080	2,2	2007, 2010, 1997, 2012	Social	3560
4	6	BZ	Amur tiger, *P. tigris altaica*	36	1080	1,1	2007, 2004	Social	1460
4	6	BZ	Cheetah, *A. jubatus*	18	540	2,0	2010 2010	Social	*540
4	6	BZ	Cheetah, *A. jubatus*	18	540	0,1,3	2008, 2015	Female with cubs	*6700
5	9	NA	Amur tiger, *P. tigris altaica*	10	360	1,0	2010	Individual	*3500
5	9	NA	Amur tiger, *P. tigris altaica*	13	360	1,0	2004	Individual	*2500
5	9	NA	Amur tiger, *P. tigris altaica*	13	360	0,1,3	2007, 2015	Female with cubs	*500
5	9	NA	Persian leopard, *P. pardus saxicolor*	36	1080	1,1	2012, 2011	Social	2100
5	9	NA	Snow leopard, *U. uncia*	36	1080	2,1	2005, 2013, 2004	Social	1950
6	9	OR	Amur tiger, *P. tigris altaica*	11	315	1,0	2008	Individual	~7000 **150
6	9	OR	Amur tiger, *P. tigris altaica*	10	315	0,1	2008	Individual	~7000 **340
6	9	OR	Persian leopard, *P. pardus saxicolor*	11	315	1,0	2009	Individual	~1700
6	9	OR	Persian leopard, *P. pardus saxicolor*	10	315	0,1	2008	Individual	~1800
6	9	OR	Snow leopard, *U. uncia*	11	315	1,0	2010	Individual	~1900
6	9	OR	Snow leopard, *U. uncia*	10	315	0.1	2009	Individual	~2000

3.3.2 Data sampling

Data sampling was made by instantaneous scan sampling every 30 second in sessions of 30 minutes. The study was divided into six observation periods where two or three species in one zoo at the time were observed by alternating between enclosures according to a balanced schedule (Table 1). Observations were performed in twelve sessions per day between 08.00 and 17.00, except for at Orsa rovdjurspark where there were seven sessions between 10.00 and 15.00. Observations were only allowed during daytime and times were regulated by the zoos opening hours.

The sessions were evenly distributed over the daytime and species so that each enclosure was observed every day during the observation period for that zoo. The order of observed enclosures was varied every day so each enclosure was observed at least once in every session number (1-12). The total amount of observed time was 229.5 hours.

Before each session time, weather conditions and visitor density were recorded. In each scan the behaviour and position of all animals in the enclosure were recorded.

Behaviours were recorded according to an ethogram (Table 2), positions and possible usage of resources were marked on a map, where the enclosure was divided into zones (Appendix 1). Because the study of enclosure usage was aiming at understanding why different areas were used rather than measuring if the whole enclosure was used the division into zones was made according to topography, geographic features etc. instead of a normal grid pattern.

Table 2. Ethogram of observed behaviours.

Behaviour	*Definition*
Running	Movement where in sequence no paw touches the ground, there is no obvious prey the individual is hunting. Trotting/galloping.
Walking	Movement where at least one paw touches the ground. Easy pace.
Jumping up or down	Movement in height.
Climbing	Movement where the cat distinctly uses paws/claws to move upward/downward.
Stereotypic pacing	Walking/running the same track over and over again (more than two turns). If the individual stops and begins another behaviour for at least three seconds it will count as a new behaviour.
Scent marking	Scratching, spraying, rolling or rubbing the cheek.
Sniffing	Contact with nose against object or surface, not other individual.
Eating	Intake of food with the mouth or using teeth to handle meat or tongue to lick e.g. egg.
Drinking	Intake of water with tongue.
Foraging	Sniffing at or on food enrichment.
Hunting	Persecution of individual of other species in/outside the enclosure, or persecution of other object.
Playing	Interacting with object or individual in an active non-aggressive manner.
Lying	No movement in any direction. On back or stomach with legs supporting the weight.
Sitting	No movement in any direction, sitting.
Standing	No movement in any direction, standing.
Grooming	Body care with mouth or paws.
Social interaction	Touching other individual with any part of the body.
Aggressive interaction	Threat, hissing, stroke with paw. Within two meters from other individual.
Other	Distinctive behaviour not defined in the ethogram.
Out of sight	Individual cannot be seen.

3.4 Statistics

Data was compiled in MS Excel 2013 and statistical analyses were carried out in IBM SPSS 23.

Data was tested for normality with a negative result in all data (Shapiro-Wilk df = 820; $P < 0.0$).

All variables were first tested for differences in mean ranks with Friedman test. All recorded behaviours were assembled into four groups; active behaviours, inactive behaviours, stereotypic behaviours and hiding. Differences between these groups of behaviours were tested with Friedman test. All groups were then tested against each other with Wilcoxon signed-rank tests and a Bonferroni adjustment of the P-value.

Resource usage was assembled into three groups; on top of elevated resource, within hiding place and nearby hiding place. Some resource usage that was very special to certain enclosures was excluded in the grouping. These groups were then tested with Friedman and Wilcoxon tests in the same way as the behaviour analysis above.

Differences in proportions of behaviours and resource usage during observation times were compared between sexes, species, social context (i.e. individual, social or female with cubs) and zoos. Since differences were analysed between two or more groups a Kruskal-Wallis analysis of ranks.

In all tests a P-value of less than 0.05 was considered statistically significant.

4 Results

4.1 Literature review

A total of 55 articles were reviewed (Appendix 2), 19 of which were rejected either for being review articles or off topic. A compilation of the remaining 36 articles is presented in Table 3.

The major focus of topics in the reviewed articles was on different types of environmental enrichment and how enrichments affect abnormal behaviours such as pacing and other stereotypes. All articles highlighted problems with keeping felids in zoos with optimal welfare. Almost all were behavioural studies but some combined behavioural studies with for instance hormonal measurements.

Nine of the reviewed articles mentioned resources such as for instance visual barriers, elevated areas and hiding boxes, or "complex environments" as factors influencing animal welfare or behaviours. The degree of welfare was foremost discussed as appearance or change in stereotypic behaviours, i.e. pacing, and cortisol levels. Either they looked at how one specific resource such as visual barriers influenced behaviours or they discussed the possibility of environmental effects. None of the articles looked into which different resources in the enclosure the animals preferred, but one studied the effect of access to hiding places and height of perches as factors influencing adrenocortical activity and welfare.

The majority of studies were performed in North America and Europe. The single article from Asia was from India. The three articles that covered Africa were in fact made by European researchers at institutions in both Europe and Africa. Szokalski and co-authors (2013) are members of an Australian research team but their study investigated the opinions of zoo keepers over the whole world. 51 % of the respondents of their online questionnaire were from the United States, 27 % from Australia and New Zealand and 11 % from Great Britain.

The sample sizes in the studies were overall small. The two articles with the largest sample sizes (n = 940, and 318) compiled data from other studies or studbooks. A few articles covered several institutions, but the studies made in only one institution typically used under 10 subjects, often just one, two or three individuals from a few different felid species and often animals housed in the same enclosure.

There was a predominance of studies made of large felid species. All species typically counted as large felids (*Panthera spp, Acinonyx jubatus, Puma concolor* and *Uncia uncia*) were represented in several studies but only 12 of the 33 extant small felid species (Orrell 2016) were represented.

Table 3.1. Compilation of data from the reviewed articles. Note that several articles covered more than one of the presented categories.
** Of the four articles with a study sample of over 100 individuals, two used compilations of other studies or studbooks, two were large multi-institutional studies.*

		no of articles	*%*
	All reviewed articles	36	100
Topics	Different types of enrichments	15	42
	Stereotypes and stressors	8	22
	Housing (social/individual, time, type)	8	22
	Behavioural patterns (size, time, visitors)	5	14
	Reproduction problems	2	6
	Personality assessment	2	6
	Visitor and keepers benefits	2	6
Resources	Resource studied	6	17
	Resource not studied	27	75
	Enclosure complexity studied/discussed	3	8
Measurements	Behaviour	33	92
	Hormones (cortisol, androgen, oestrogen)	8	22
	Keepers opinions	3	8
	Infant mortality, breeding success	2	6
	Visitor numbers	2	6
	Distance covered	1	3
	Run speed	1	3
Location	North America	16	44
	Europe	13	36
	South America	4	11
	Africa	3	8
	Central America	2	6
	worldwide	2	6
	Asia	1	3
Study sample*	≥100	4	11
	≥20	6	17
	≥10	13	36
	<10	15	42

*Table 3.2. Compilation of data from the reviewed articles. Note that several articles covered more than one of the presented species and categories. *Big felid species consist of* Panthera spp*,* Acinonyx jubatus*,* Puma concolor *and* Uncia uncia*, all other felid species are regarded as small.*

			no of articles	*%*
Species	Tiger	*Panthera tigris*	12	33
	Cheetah	*Acinonyx jubatus*	7	19
	Lion	*Panthera leo*	6	17
	Snow leopard	*Uncia uncia*	5	14
	Leopard	*Panthera pardus*	2	6
	Jaguar	*Panthera onca*	3	8
	Margay	*Leopardus wiedii*	3	8
	Oncilla	*Leopardus tigrinus*	3	8
	Clouded leopard	*Neofelis nebulosa*	2	6
	Cougar	*Puma concolor*	2	6
	Ocelot	*Leopardus pardalis*	2	6
	Bobcat	*Lynx rufus*	1	3
	Canada lynx	*Lynx canadensis*	1	3
	Fishing cat	*Felis viverrinus*	1	3
	Geoffroy's cat	*Leopardus geoffroyi*	1	3
	Jagarundi	*Puma yaguarondi*	1	3
	Serval	*Leptailurus serval*	1	3
	Tigrina	*Leopardus guttulus*	1	3
	*Big felid species		28	78
	Small felid species		12	33

4.2 Examination of practiced husbandry

Four husbandry guidelines were reviewed; Husbandry Manual for the Cheetah *Acinonyx jubatus* (Ziegler-Meeks 2009), EAZA Leopards *Panthera pardus spp.* Husbandry Guidelines (Houssaye & Budd 2009), Pallas's cat EEP Husbandry Guidelines (*Otocolobus manul*) (Barclay 2013) and EEP-Husbandry Recommendations for Tigers (*Panthera tigris*) (Richardson & Lewis 2010).

Although they covered such different felid species as the tiger, leopard, cheetah and Pallas's cat, these four husbandry guidelines varied greatly in scope but were similar in content when it came to housing, enclosure design, enrichments and feeding.

Even though these species have been kept in zoos worldwide for a long time, knowledge about physiology and nutrition are foremost based on the house cat. All but one of the guidelines were six or seven year’s old and when references were cited these were even older, the majority of them from the 1990’s.

4.2.1 Housing

All felid species except lions and male cheetahs are traditionally considered as solitary animals with little contact with conspecifics between mating times. The husbandry guidelines recommended zoos to keep felids either individually or, in contrast to the situation in the wild, in social groups when it is possible.

The tiger guidelines recommended family groups, with male, female and their offspring, except during the cubs’ first four weeks. The Pallas’s cat guidelines advised zoos to keep the cats individually or in pairs but separate the female prior to parturition and during kitten rearing periods. If the Pallas’s cats are kept either in pairs or possibly in one-sex sibling groups the guidelines stated that there should be many nest boxes and hiding places to enable privacy for the individual cats. The leopard guidelines stated that female groups established in pre-adulthood might work but male groups are a great risk. On the contrary, the cheetah guidelines recommended that full sibling brothers should be allowed to stay together. Female groups and mixed pairs/groups were only recommended for non-breeding individuals since living in groups or mixed pairs might lead to reproductive suppressions as reported by Wielebnowski *et al.* (2002).

4.2.2 Enclosure design

All four guidelines stated that enclosures should be naturalistic and as large as possible. Some mentioned that governmental minimum space requirements are generally too small to be used as proper guidelines. Important to note here is that many countries even in Europe do not have minimum space requirements. The guidelines also stated that complexity is important and there should be elevated resting and hiding places, shelter from sun, wind and rain and sight barriers so that the animals can escape both visitors and conspecifics. Natural behaviours should be encouraged by the enclosure design. There should be several nest boxes allowing the female to move her kittens or cubs. The enclosure should be safe enough to allow the animals to be outside also during the nights to prevent long periods in small back enclosures or indoor pens. According to the cheetah guidelines cheetahs should be allowed to have visual contact with hoofed animals.

4.2.3 Feeding

All four guidelines agreed that whole carcasses are good not only for proper nutrition but also as a way to provide the animals with means to perform natural behaviours. A variation of whole small animals such as chicken, rats, rabbits and quails were recommended for the Pallas's cats but they should be frozen and thawed prior to feeding to reduce the risk of toxoplasmosis contamination.

It is a common practice in many zoos to subject the felids to starve days as a way to control overweight in inactive animals and to imitate natural conditions where the wild animals do not succeed to catch their prey every time. However, Richardson & Lewis (2010) stated in the husbandry guidelines for tigers that this practice is not appropriate and might increase stereotypic behaviours.

4.2.4 Enrichments

Enrichments should be varied and promote natural behaviours. The cheetah guidelines listed three main goals with enrichments; 1) to promote species appropriate behaviours; 2) to provide a wide range of behavioural opportunities for each category of behaviour; 3) to provide animals with control over their environment (Ziegler-Meeks 2009).

The four guidelines listed varying food presentations and different play objects for stimulating hunting behaviours, olfactory stimulation, novel objects and change of enclosures for investigating behaviours, social housing or animal/keeper interactions as examples of enrichments. They stated that to facilitate opportunities to move and exercise is important to prevent passivity, stereotypic behaviours and overweight. This can for instance be accomplished with a lure track for the cheetahs, climbing trees or an unstable but safe climbing pole.

Ziegler-Meeks (2009) also promoted the use of a well-planned enrichment program following procedures such as for instance SPIDER (Setting goals, Planning, Implementing, Documenting, Evaluating, Readjusting).

4.3 Behavioural observations

In summary the behavioural observations showed that all felids, summarised together, were mostly resting or inactive during the observations, although there were individual differences. Stereotypic pacing occurred in all species except the Pallas's cats. They were on the other hand to a higher degree hiding. High perches were the most used resources overall. All females summarised used hiding places more than males and Pallas's cats used hiding places most of all species. The usage of hiding places changed with time of day but not usage of the other resources.

4.3.1 Behaviours

The most common behaviour observed was lying, followed by walking, standing, sitting and pacing (Figure 1). Pacing was seen in 20 of the 34 (59 %) individuals observed in the study. Two individuals stood out with exceptionally high levels of pacing, comprising 37 and 25 % of the observed time respectively, the other 18 ranged between 12 and 0.1 % of the observed time.

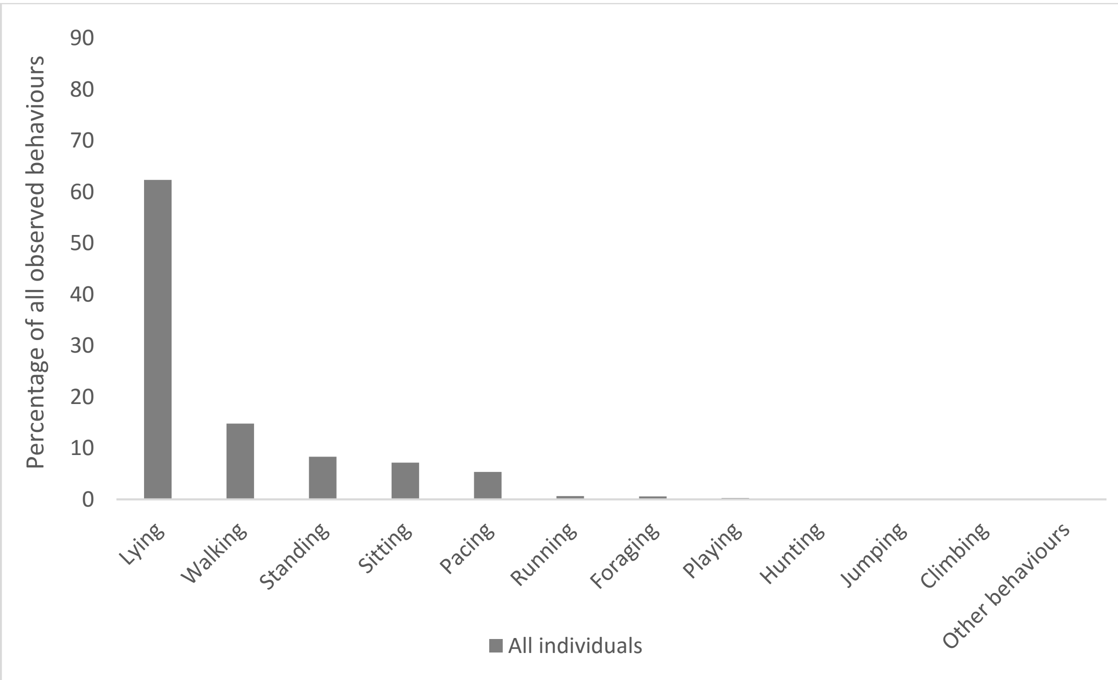

Figure 1. Proportions of observed stand-alone behaviours in the whole study sample. Behaviours possible to combine with these such as grooming have been excluded from the data.

For further comparisons the behaviours were grouped into active behaviours (all movements except pacing), stereotypic behaviours (pacing), inactive behaviours (lying, sitting and standing) and hiding (out of sight).

There was a statistically significant difference in performed behaviours tested in these four groups ($\chi2_{(3)} = 1136.3$, $P < 0.0$). A post hoc analysis of differences between behaviour groups with Wilcoxon signed-rank tests showed that differences between all groups of behaviours were significant. Active/inactive behaviours ($Z = -21.6$, $P < 0.0$), active/stereotypic behaviours (Z 0 -14.0, $P < 0.0$), active behaviours/hiding ($Z = -3.6$, $P < 0.0$), inactive/stereotypic behaviours ($Z = -22.9$, $P < 0.0$) inactive behaviours/hiding ($Z = -16.8$, $P < 0.0$) and stereotypic behaviours/hiding ($Z = -9.3$, $P < 0.0$). A Bonferroni correction resulted in a significance level at $P < 0.008$.

Although performed behaviours did not differ much when comparing male and female behaviours a Kruskal-Wallis test showed that there were statistically significant differences in ranked means between sexes in active behaviours ($\chi2_{(1)} = 7.6$, $P < 0.0$), stereotypic behaviours ($\chi2_{(1)} = 6.3$, $P < 0.0$) and hiding ($\chi2_{(1)} = 5.5$, $P < 0.0$) but not in inactive behaviours. Behaviours according to sex are presented in Figure 2 as proportions of observed behaviours.

Figure 2. Behavioural differences between males and females as proportions of observed behaviours. The behaviours were grouped into active behaviours (all movements except pacing), stereotypic behaviours (pacing), inactive behaviours (lying, sitting and standing) and hiding (out of sight).

When behaviours were compared between species there were more differences (Figure 3), especially the Pallas's cats distinguished themselves from the other species by being much more in hiding and less active. Cheetahs were more active than the other species. A Kruskal-Wallis test showed that differences were statistically significant in all combinations ($\chi2 = 6.0$, $P < 0.0$).

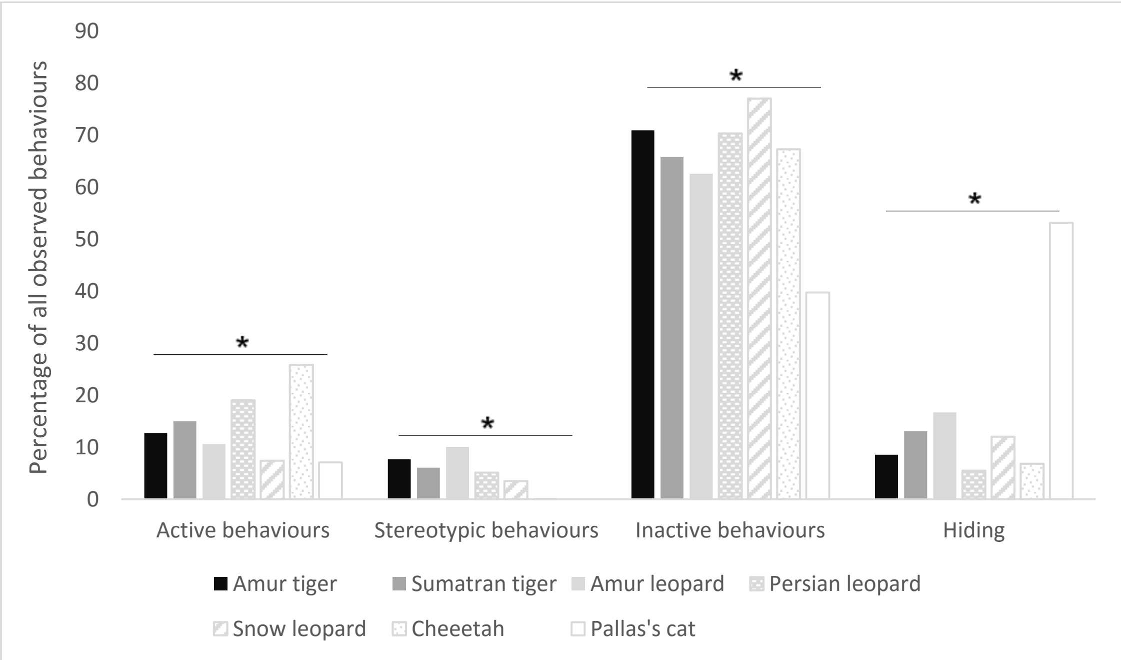

Figure 3. Behavioural differences between the species included in the study as proportions of observed behaviours. The behaviours were grouped into active behaviours (all movements except pacing), stereotypic behaviours (pacing), inactive behaviours (lying, sitting and standing) and hiding (out of sight).

Although felids are considered solitary animals a majority of the individuals in the study were kept in enclosures together with one or more conspecifics. In a comparison between social contexts the three females with kittens or cubs were singled out as a special group since the young ones affect the behaviour of the mother (Figure 4). When testing all three categories with a Kruskal-Wallis test, only differences in stereotypic behaviours were significant ($\chi2_{(1)} = 30.5$, $P < 0.0$) but when the females with cubs were excluded the inactive behaviours were also found to be significantly different ($\chi2_{(1)} = 5.1$, $P < 0.0$).

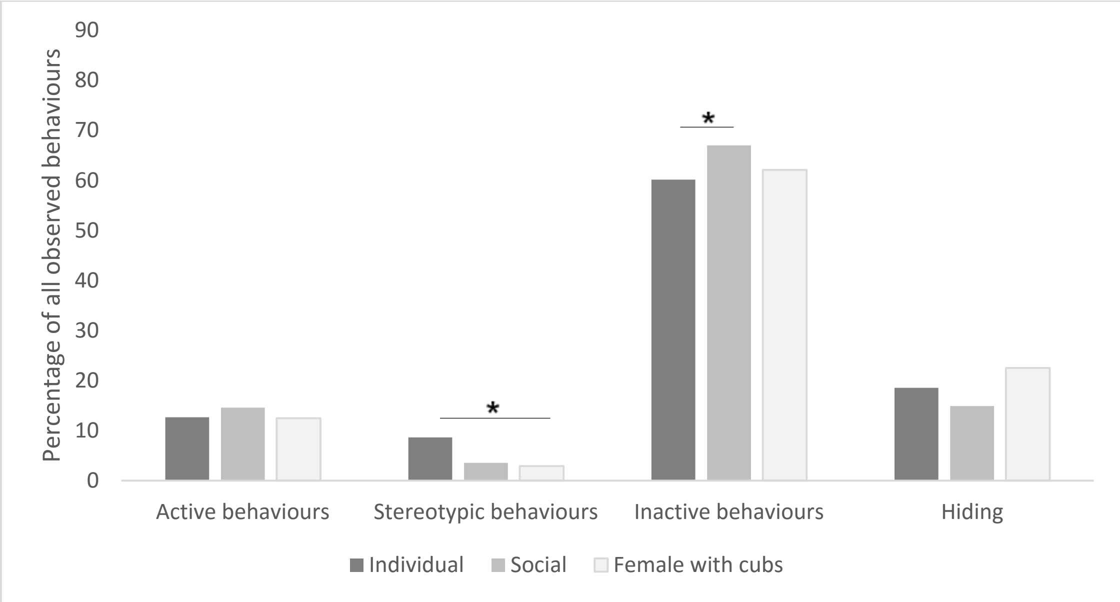

Figure 4. Behavioural differences between individuals in different social contexts as proportions of observed behaviours. Individuals were grouped in individual (individually kept) social (two or more together in one enclosure) and female with cubs (a single female with cubs or kittens). The behaviours were grouped into active behaviours (all movements except pacing), stereotypic behaviours (pacing), inactive behaviours (lying, sitting and standing) and hiding (out of sight).

4.3.2 Use of resources

All felids pooled together used some kind of resource in their enclosures 42 % of the observed time. Which resources the animals had access to naturally differ between all enclosures but all of them had access to some kind of elevated resting places and varying hiding places. Resource usage were divided into three groups; on top of elevated resource, in hiding place (within hut, hollow log or under a bush), nearby hiding place (such as when the animal sat next to a hut or behind a bush in a hiding manner).

There were statistically significant differences in use of resources in the three groups ($\chi2_{(2)} = 329.2$, $P < 0.0$). There were also significant differences between all groups of resources when tested with the Wilcoxon signed-rank test against each other. On elevated resource/in hiding place ($Z = -6.4$, $P < 0.0$), on elevated resource/nearby hiding place ($Z = -14.0$, $P < 0.0$) in hiding place/nearby hiding place ($Z = -7.8$, $P < 0.0$). A Bonferroni correction resulted in a significance level at $P < 0.017$.

Perching on top of an elevated structure of some kind was the most common resource usage in both the whole study sample and compared between sexes (Figure 5). The Kruskal-Wallis test showed that the differences between sexes in on top of elevated resource ($\chi2_{(3)} = 8.7$, $P < 0.0$) and within hiding place ($\chi2_{(3)} = 8.7$, $P < 0.0$) were significant but not nearby hiding place.

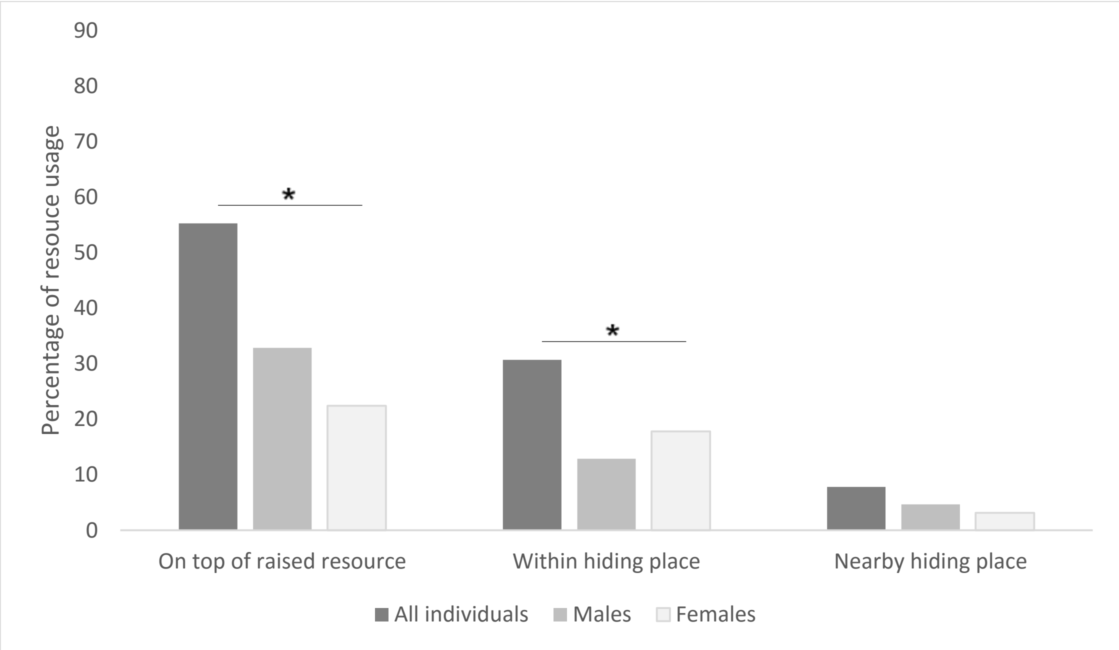

Figure 5. Proportion of resource usage within the whole study sample and divided between sexes. Resource usage were grouped as; on top of an elevated manmade resource, boulder, cliff ledge etc., within a hiding place such as a hut, hollow log or under a bush, and nearby hiding place when the animal used the resource in a hiding manner but behind or next to instead of within.

Both leopard species and the snow leopards' used elevated resources more than hiding places while the Pallas's cats clearly preferred hiding places. Tigers and cheetahs did not differ as much between the usages of these two types of resources (Figure 6). All three categories of elevated resource, within hiding place and nearby hiding place differed significantly according to the Kruskal-Wallis test (elevated resource $\chi2_{(6)} = 155.2$, $P < 0.0$; within hiding place $\chi2_{(6)} = 144.4$, $P < 0.0$; nearby hiding place $\chi2_{(6)} = 21.5$, $P < 0.0$).

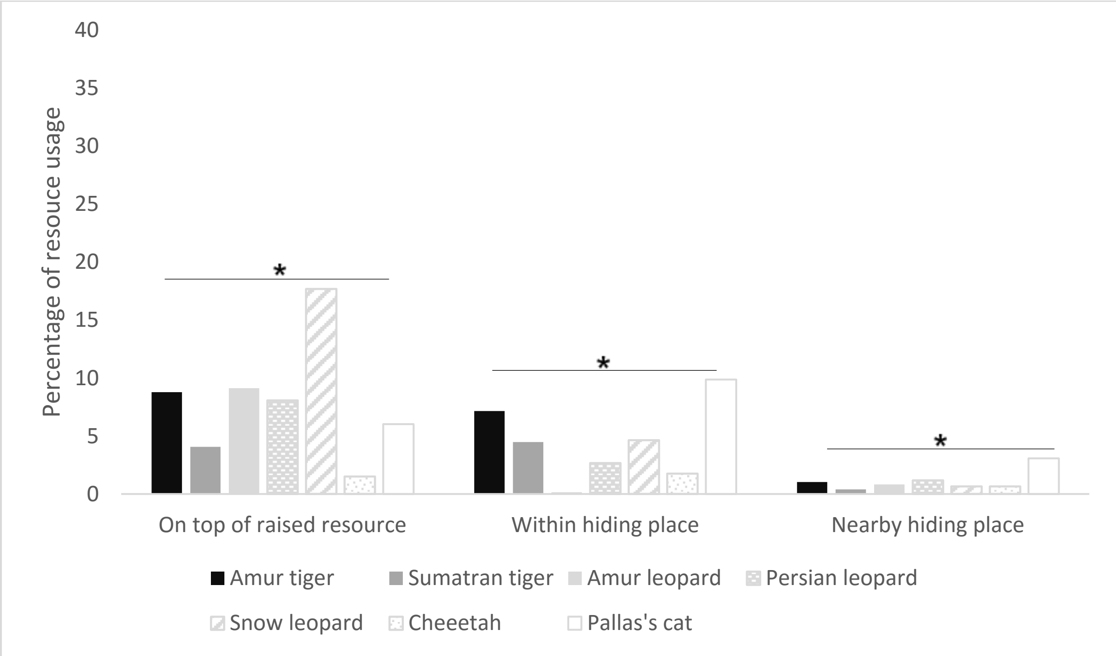

Figure 6. Proportion of resource usage between species in the study. Resource usage were grouped as; on top of an elevated manmade resource, boulder, cliff ledge etc., within a hiding place such as a hut, hollow log or under a bush, and nearby hiding place when the animal used the resource in a hiding manner but behind or next to instead of within.

When comparing resource usage within different social contexts there was a significant difference in all three categories, elevated resource ($\chi2_{(2)}$ = 11.1, P < 0.0), within hiding place ($\chi2_{(2)}$ = 30.1, P < 0.0) and nearby hiding place ($\chi2_{(2)}$ = 15.1, P < 0.0) (Kruskal-Wallis test). Both in use of elevated resources and within hiding places the social group stand out with high peaks (Figure 7).

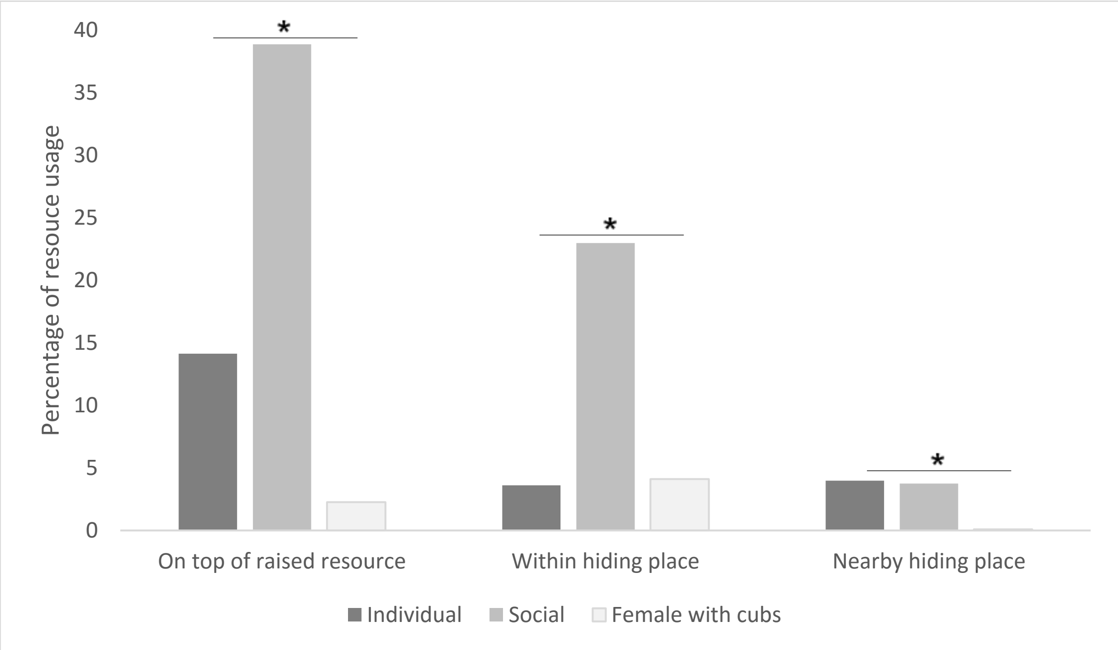

Figure 7. Proportion of resource usage between individuals in different social contexts. Individuals were grouped in individual (individually kept) social (two or more together in one enclosure) and female with cubs (a single female with cubs or kittens). Resource usage were grouped as; on top of an elevated manmade resource, boulder, cliff ledge etc., within a hiding place such as a hut, hollow log or under a bush, and nearby hiding place when the animal used the resource in a hiding manner but behind or next to instead of within.

To see if the usage of resources varied over time the observation days were divided into quarters (Figure 8). According to the Kruskal –Wallis test only the category within hiding place was significantly different ($\chi 2_{(3)}$ = 8.7, P < 0.0).

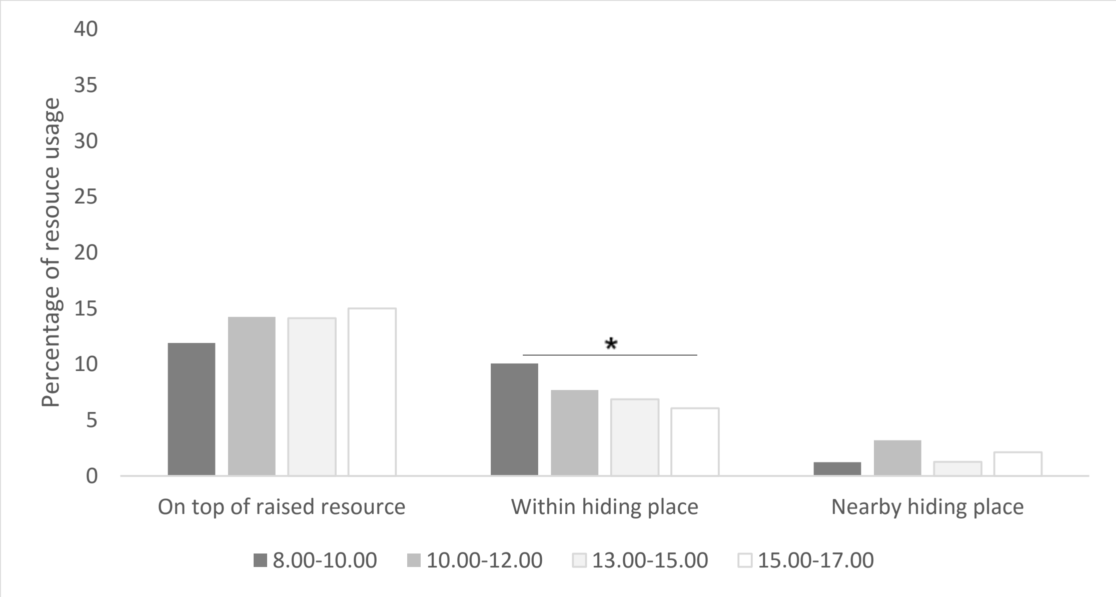

Figure 8. Proportion of observed resource usage during different times of the day. Resource usage were grouped as; on top of an elevated manmade resource, boulder, cliff ledge etc., within a hiding place such as a hut, hollow log or under a bush, and nearby hiding place when the animal used the resource in a hiding manner but behind or next to instead of within.

4.3.3 Use of enclosures

Approximately two thirds of the individuals in the study were kept in enclosures where not only structures gave access to an elevated resting place, but the ground level varied into areas with a distinct elevation above other parts of the enclosure and the public viewing points. When analysing the usage of these elevated areas only those individuals that had access to such were counted (Figure 9). The Kruskal –Wallis tests showed that differences between species ($\chi2_{(5)} = 44.3$, $P < 0.0$) and social context ($\chi2_{(2)} = 15.8$, $P < 0.0$) were significant but not between sexes and zoos.

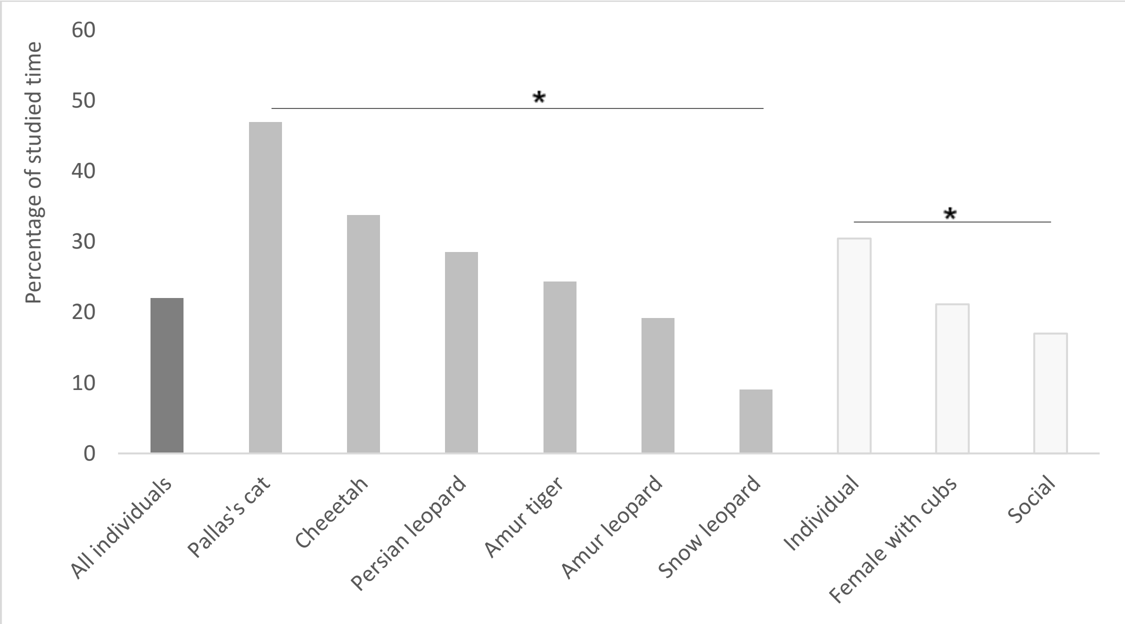

Figure 9. Proportion of usage of areas within the enclosures with a ground level higher than the public viewing points. Only individuals with access to such elevated areas were included in the analysis. Manmade resources were not counted as elevated areas. Result presented from left to right as all individuals, divided in species and divided according to social context. Social contexts were grouped in individual (individually kept) social (two or more together in one enclosure) and female with cubs (a single female with cubs or kittens).

To see if the animals moved in a small area or used the whole enclosure, the number of zone changes was measured for each individual. Mean number of zone changes in all groupings are presented in Figure 10. Because the enclosures sizes varied the mean number of zone changes have been normalised to enclosure size. All three cheetah males frequently patrolled their enclosures unlike the snow leopards which were more seldom observed moving around.

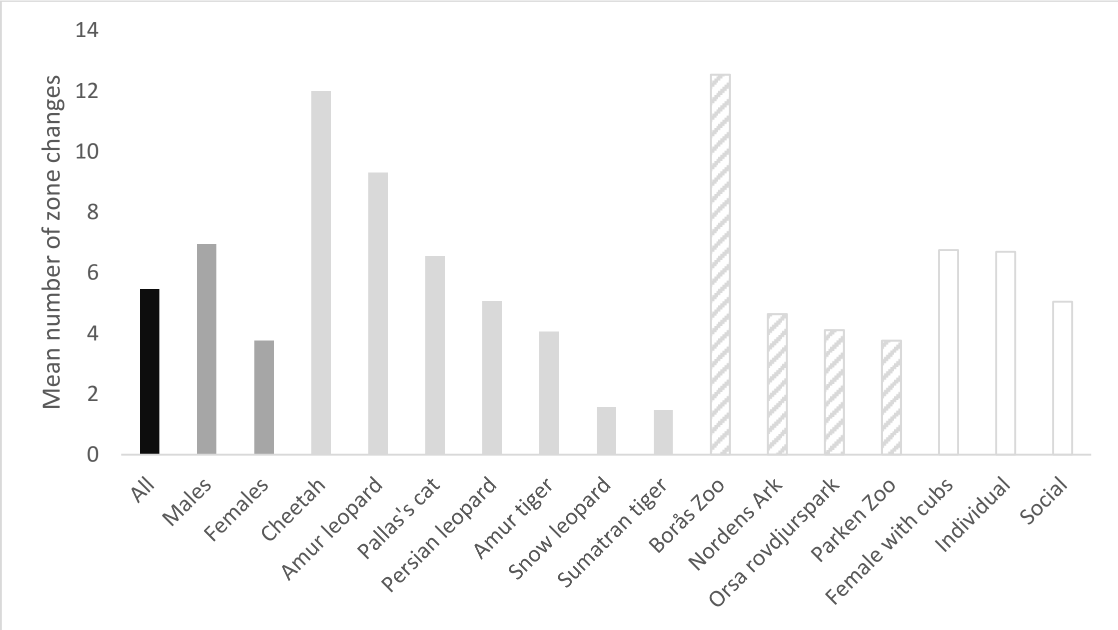

Figure 10. All enclosures within the study were divided into smaller zones and number of zone changes each individual performed per session counted. Presented as mean number of zone changes, normalized to enclosure size.

The number of zone changes varied over time but analysed in combination with time of day there were only individual patterns. For instance, the cheetahs moved around more during the early sessions shortly after being released outside or into another enclosure. The adult snow leopard male at Nordens Ark moved around more while the female and especially the juvenile male stayed in one place.

The use of the enclosures itself and not just the resources was also of interest when trying to distinguish what the felids preferred in their captive environment. Since the enclosures varied both in size and layout every enclosure have been analysed separately in this part. Most used enclosure zones are marked on the maps in Appendix 1.

The Amur tigers at Borås Zoo used their manmade resources often and were mostly in the zone where these were. The Amur tigers at Nordens Ark and at Orsa rovdjurspark had access to higher ground and often utilised this but the tigers at Nordens Ark also spent much time in the cage locks. The four Sumatran tigers at Parken Zoo used the whole enclosure. They were often seen separate but in close vicinity to each other and two of them had clear favourite resting spots, in one of the huts and in a secluded corner by the fence.

The Amur leopards mostly rested on high ground or perches except the females at Parken Zoo which were lying more or less out of sight close to the wall or indoors. The Amur leopards at Nordens Ark were pacing in the areas closest to the conspecific’s enclosure. The Persian leopards at Nordens Ark rested high up while the Persians at Orsa rovdjurspark chose the ground. The female Persian leopard at Orsa rovdjurspark was mostly hidden and the male patrolling the whole enclosure. All snow leopards were mostly inactive and chose either elevation or hiding as they rested.

All cheetahs had favourite resting spots where they were a large proportion of the observation time even though especially the males also patrolled their enclosures a lot. All of them chose ground level for resting except the female cheetah at Borås Zoo. She spent most of her time in the safe area where the rhinoceroses could not go. This was also the area where the hut was situated which she used both by lying inside and by sitting on top of it.

The Pallas’s cats were much more out of sight than the other felids both at Nordens Ark and Parken Zoo. In contrast to the other felids they had huts and hiding places where they were completely out of sight. When they were seen they preferred to rest on top of high ground or structures.

5 Discussion

5.1 Literature review

When reviewing published articles for knowledge of felid welfare and resource usage among different species of felids the aim was to see if such knowledge is lacking.

Indeed none of the reviewed articles was about the use of resources.

Stereotypic behaviours are considered signs of frustration and reduced welfare in zoo held animals due to hindrance in performing natural behaviours (Mason & Latham 2004). Stereotypic behaviours in herbivores are usually linked to the inability to feed properly and naturally since they normally spend a majority of their time foraging and feeding (Bergeron *et al*. 2006).

Traditionally stereotypic behaviours, most commonly pacing, in carnivores have been linked to the inability to hunt and feed naturally as well (Mason *et al*. 2007, Morgan & Tromborg 2007). Clubb & Mason (2007) challenged this view when they showed that pacing in carnivores was more rooted in natural home range size than inability to hunt and feed naturally. Providing properly sized enclosures is always a problem when keeping animals in zoos. In the wild many felid species cover large areas every day when patrolling their home ranges (Sunquist & Sunquist 2002). On the other hand, even within species home ranges vary greatly depending on access to resources, and conspecific and prey population density (Benson *et al*. 2006, Cascelli de Azevedoa & Murrayc 2007). How can we find the limit for when the area size starts to affect the animal when even in zoos with huge enclosure areas it is far from the size of the felids' natural home ranges? Also, there is most probably a great individual variation as well as differences between felid species.

Large, complex enclosures, sufficient hiding places, different types of environmental enrichments have been shown to have negative correlations with the occurrence of stereotypic behaviours but neither completely removes the abnormalities or have a long-standing effect (e.g. Clubb & Mason 2007, Morgan & Tromborg 2007, Miller *et al*. 2008). Meagher & Mason (2012) found caged mink to have a negative affective state caused by under-stimulation, consistent with the human state of boredom. The bored minks were inactive but awake, and had an elevated interest in any stimuli. The authors also found an indication that stereotypic behaviours might help the animals to alleviate boredom.

Fanson & Wielebnowskis (2013) found that the three most important factors correlated with adrenocortical activity, i.e. stress, in Canadian lynx, where size of enclosure, number of hiding places and social housing. Moreira *et al*. (2007) found in their study that stress hormone levels increased when the animals were moved from large complex enclosures to small barren but returned to baseline again when the small enclosures were furnished. With that in mind boredom, limited ability to use all senses and lack of proper hiding places might be just as important factors as restricted areas.

We need to study all these other factors. It is clear that to this day both zoo managements and researchers have been concentrating most efforts on trying to prevent or reduce stereotypic behaviours by environmental enrichments but in spite of numerous studies we fail to completely understand and prevent stereotypic behaviours. We need to explore other solutions, such as for instance which resources the felids need or prefer in their environments.

The reviewed articles were highly unbalanced when it comes to the species studied. All of the large felid species are well studied both in captivity and in the wild but for many of the smaller felid species knowledge is missing (Inskip & Zimmermann 2009). Even though many behaviours and needs are similar in all felid species there are differences in for instance social structure, habitat use, home range and not the least whether or not the animal is also a prey animal. In addition to welfare discussions there is a great need to gather more knowledge about the smaller felids in order to conserve the species since a large number of these felid species are vulnerable, threatened or have not been assessed in several years (IUCN 2014).

One of the major problems with studies performed on zoo kept animals is that the sample size often is very limited. When studying behaviours and welfare problems this is unfortunate since all individuals react according to personality, environmental circumstances, upbringing, health and other factors and it is difficult to find hard evidence or generally applicable results. Long-term multi-institutional studies are therefore desirable. Stanton *et al*. (2015) recently presented a standardized ethogram for felid species which might improve synchronization of behavioural studies in the future.

5.2 Examination of practiced husbandry

The second aim of this study was to review husbandry guidelines to find out if new research findings had been conveyed to the zoo communities and hence if the practiced husbandries are founded more on scientific findings, rather than traditions and anecdotal knowledge.

Even though all felid species except lions and male cheetahs are traditionally considered as solitary animals all four guidelines recommend social housing to a certain degree. According to Freeman (1978) wild snow leopards have been observed living or hunting in stable pairs. De Rouck *et al*. (2005) reviews several reports of wild tigers sighted in social contact with conspecifics outside of mating times. Sliwa (2004) found that a pair of sisters of black-footed cats (*Felis nigripes*) although living solitary shared almost half their home range. Feral cats (*Felis silvestris catus*) form colonies (Crowell-Davis *et al*. 2004). These examples indicate that the solitary lifestyle is not absolute and that there is a varying degree of contact between different individuals and in different species of felids.

According to Houssaye & Budd (2009) there is a common opinion in the zoo community that felids kept in social groups can benefit from this by being able to perform more natural behaviours, both affiliate and agonistic behaviours. Visitors also like to see animals together (Houssaye & Budd 2009). Since humans are very social animals, people tend to feel that no animals should be alone. And thirdly it is easier for the zoo to keep an established breeding pair together (Houssaye & Budd 2009).

It might very well be that some felids benefit from social holding but it is important to evaluate each individual to see which enjoys company and which does not. Fanson & Wielebnowski (2013) found in their study that one of the three most important welfare factors was group size and composition, where lynx in groups of three or more and especially in mixed sex groups had a high adrenocortical activity compared to lynx housed alone. De Rouck *et al*. (2005) concluded that tigers should preferable be kept in pairs or small groups for a satisfactory welfare, but conspecifics in neighbouring enclosures constitute a stressor. In agreement Miller *et al*. (2008) also found a significant reduction of pacing after a visual barrier between neighbouring enclosures with conspecific tigers was erected. Chadwick e*t al.* (2013) suggest that keeping male relatives of cheetahs together might improve welfare and reproduction success while Wielebnowski *et al*. (2002) found that keeping female cheetahs and possibly even breeding pairs in constant company might lead to welfare problems and suppressed ovarian cyclicity.

Even though there are few studies about resource utilisation all husbandry guidelines (Houssaye & Budd 2009, Ziegler-Meeks 2009, Richardson & Lewis 2010, Barclay 2013) recommend that there should be complexity, elevated resting places, shelters and sight barriers in the enclosures.

Lyons *et al*. (1997) and Bashaw *et al*. (2007) found that felids showed different behaviours and activity levels in large enclosures compared to small enclosures. Moreira (2007) found that the complexity within the enclosure was as important and Lyons *et al*. (1997) found that in large enclosures less of the enclosure space was used. Even large zoo enclosures are small in comparison with the natural home ranges of felids and most zoos have not enough space for larger enclosures. Therefore it is important to know why the felids prefer some areas and resources to other.

Morgan & Tromborg (2007) state that to be in control of their situation and have the ability to hide and retreat from both humans and conspecifics is highly important for the welfare and ability to cope with different stressors in most captive wild mammals. A good overview of the surroundings and easily defended resting places are therefore preferable. It is well documented that domestic cats often choose high resting places (Rochlitz 2005). Lyons *et al*. (1997) found this to be true also with other felid species in Edinburgh Zoo. If no elevated objects were present the animals mostly choose the back high end of the enclosure. According to Lyons *et al*. (1997) using the back end of a sloping enclosure might be a way to both place oneself at the highest point in the enclosure but also to be at the farthest distance to the visitors.

Fanson & Wielebnowski (2013) saw that the number of hiding places was important for welfare in lynx. In a study of domestic cats in a shelter Vinke *et al*. (2014) found that access to hiding places strongly affected the cats' ability to cope with the stressful environment.

Thorough research on which resources the zoo felids prefer and if this differ between species is lacking and there is probably also an individual variation in preferences. In order to increasing the felids control of their situation one might assume that it is not only important to provide the animals with proper resources in the enclosure but also to provide them with several options.

To simulate natural conditions with failed hunting and to control overweight it is common to not feed the larger felids every day. The tiger guidelines recommend zoos to move away from this practise of starving days since it might increase stereotypic behaviours. This statement is supported by the findings of Lyons *et al*. (1997), that pacing levels were higher on starving days than feeding days. Interestingly the effects of starving days are not much investigated although it is quite a common practice in zoos. Lindburg (1988) identified four phases of feeding behaviours in felids; locating, capturing, killing and processing. Since zoo animals are not able to perform these stages of feeding, enrichment programs are launched to simulate all these phases of feeding behaviours.

All four guidelines recommend enrichment programs to promote natural behaviours and most of the reviewed scientific articles studied the effects of different types of enrichment or enrichments practices. The guidelines do not specify which type or degree of enrichments. Quirke *et al*. (2011a) found that by altering time and place for feeding, together with olfactory enrichments, the frequency and number of natural behaviours increased and pacing decreased. When a randomised schedule of the enrichments was introduced these effects were even greater (Quirke *et al*. 2011b). Skibiel *et* *al*. (2007) found that enriching with bones, spices and fish frozen in ice affected activity and pacing differently in different species of felids although the study sample was too small for clear statistically valid generalisations.

In the recommendations on enclosure design and furnishing only one guideline has scientific references, from 1996. Although the majority of animal welfare research in zoos studies the effects of different enrichments the guidelines have no scientific references about enrichments or references are as old as from the 1990's. It was not possible to find scientific research in agreement with all recommendations. This points to the conclusion that guidelines are based more on anecdotal than on scientific knowledge. Zoo practises also tend to be done as they always have been and attitudes towards routines to be based on tradition, not the least since the guidelines are not updated very often. Even though there are research going on, it is often on a small scale with just a few animals and provides results that are hard to generalise. Husbandry practice and attitudes differ sometimes substantially even in cultures as similar as between US and Europe, such as for instance feeding regimes with more processed commercial food used in USA and whole carcasses used in Europe (Ziegler-Meeks, 2009). Communicating new research findings and overcoming different cultural attitudes might be very hard without results which can be generalised.

As one of four goals for their members, EAZA lists research of all aspects of animal biology, in order to improve the understanding of animals and how they live and interact (EAZA, 2015). As a part of the organisational structure there is a specialist research committee, and from 2013 EAZA run the peer-reviewed Journal of Zoo and Aquarium Research (JZAR) as a forum for publication of new research, reviews, technical reports and evidence-based case studies (JZAR, 2016). That the husbandry guidelines are not updated more often and do not use the latest research findings indicates a non-efficient communication within the EAZA organisation. In order to obtain an efficient communication between researchers and zoo management, EAZA would need to investigate the flow of information within the organisation.

There is a large body of knowledge within the zoo community which could be used to improve and expand scientific research, for instance through questionnaires to the zoo keepers, by using logged data of enrichment programs, feeding and breeding etc.

5.3 Behavioural observations

The hypothesis for the behavioural study was that even though behaviours might be similar in all felid species, the use of, and need for, certain resources probably differ between species. Several other factors and individual preferences are likely also important in the choice of resources why it might not be possible to distinguish a general priority of resources.

5.3.1 Behaviours

The most common behaviour observed in all species and individuals was lying (Figure 1) which is not surprising since the observations were performed during daytime and felids are mostly active from dusk to dawn (Sunquist & Sunquist 2002). In addition to stereotypic behaviours, felids might respond to captivity and sub-optimal welfare by being passive and/or hiding (Carlstead *et al*. 1993, Morgan & Tromborg 2007, Chosy *et al*. 2014, Fureix & Meagher 2015). Therefore it is important to study the felids daytime resting behaviour as well as crepuscular and nocturnal activity. It is hard to distinguish whether the resting is due to natural behaviour or passivity and therefore it is possible that welfare problems could be neglected if passivity is missed. Behaviours differed somewhat between the species observed here as the Pallas's cats never performed any stereotypic pacing and were more in their hideouts than the other species (Figure 3). This indicates that small felid species such as the Pallas's cats use hiding rather than pacing as a way of coping, but because the Pallas's cat were the only small felid species included in the study this could also be a species-specific behaviour. A small felid is also in risk of being a killed by larger carnovores (Donadio & Buskirk 2006) which would affect the evolution of their species-specific behaviours. The Pallas's cats were seldom out in the open during observations and kept close to their hiding places. In the wild Pallas's cats are known to spend the days resting in caves or burrows, or sunning in a sheltered place, and becoming more active in the late afternoon and evening (Sunquist & Sunquist 2002). Moreira *et al*. (2007) found in their study of oncillas and margays that these cats spent most of the daytime resting on branches or hiding in their nest boxes, and both stereotypic behaviours and other activity increased during the night time. For small felids it is probably more important with several hiding places and coverage above and around their resting places in the enclosure so that they can feel secure during the days.

The cheetahs were more active than the other species (Figure 3), often seen patrolling their enclosures and watching other animals in neighbouring enclosures. Closeness to other species as well as conspecifics in neighbouring enclosures affects the behaviour and welfare of felids. Both De Rouck *et al*. (2005) and Miller *et al*. (2008) found that conspecifics in close proximity without sight barriers were stressful for tigers. Both Amur leopards at Nordens Ark were pacing in the areas closest to the conspecific's enclosure. The cheetah guidelines state that cheetahs should have viewing access to hoofed animals. In the cheetah exhibit at Borås Zoo there were elevated viewing points with visual access to the savannah in one direction, tigers and apes in the other. The female cheetah was observed taking advantage of this several times. The cheetahs at Parken Zoo were seen observing and stalking the neighbouring alpacas and ostriches multiple times. Both these occasions seemed stimulating for the felids. On the other hand the Sumatran tigers at Parken Zoo were often pacing along the fence to the dholes indicating a less beneficial contact.

There were also differences in behaviour depending on the animals being kept in social groups or not, with animals in a social situation performing less pacing and being more inactive (Figure 4). Even though felids are mainly solitary animals they seem to benefit from being held in social groups as they then are stimulated to perform more natural behaviours, but they might also react with more passive behaviours. Miller *et al*. (2011) concluded in their study that tigers kept in small enclosures together with conspecifics became more inactive in order to avoid aggressive encounters.

It is important for felids to control their environment by for instance patrolling their home range or enclosure, to scent mark and to check for markings and signs of rivals or prey (Clubb & Mason 2007, Lewis *et al*. 2015). It is often hard to distinguish between patrolling and pacing. One can for instance speculate whether or not the Persian leopard male at Orsa rovdjurspark, which was observed patrolling his enclosure over and over again, was in the same state of mind as the pacing animals. It could be a form of pacing even though it does not fit the definition in the ethogram.

The cheetahs were also often observed patrolling. These animals were kept in other enclosures during the night, the cheetahs at Parken Zoo indoors and those at Borås Zoo changed enclosures with other conspecifics. The patrolling was more intensive during early sessions in consistence with this being a natural behaviour and them re-familiarising themselves with their enclosure.

It is common practice in many zoos to house felids in indoor or back enclosures during the night (e.g. Mallapur & Chellam 2002; Richardson & Lewis 2010; Miller *et al*. 2013). The Amur tigers at Orsa rovdjurspark were kept indoors and in a small back enclosure during the nights. All felids at Orsa rovdjurspark were fed indoors. The Persian leopards and snow leopards had very recently been admitted free access to both indoor and outdoor enclosures during the nights but had prior to this been kept indoors. The cheetahs at Parken Zoo were kept indoors during the nights, either together as they were in the outdoor enclosure or separated. The leopards and tigers at Orsa rovdjurspark were separated all the time but in close contact through the mesh fence with the conspecific of the other sex both indoors and outdoors. Miller *et al*. (2013) saw no negative effects of alternating overnight routines between social and individual holding in tigers.

In this study no felids were observed in their indoor enclosures or at night time so their behaviours during these times are unknown. As discussed above, felids are most active during night time. To then keep them in an even smaller area during their most active period might have a negative impact on their welfare. Mallapur *et al*. (2002) found a significantly higher level of stereotypic pacing during night housing than in the exhibit enclosures. It is not possible from the results in this study to correlate any daytime behaviours with night housing regimes.

Stereotypic behaviours, foremost pacing, are common in zoo kept felids (Clubb & Mason 2007). Out of 34 individuals in this study, 59 % were observed pacing. Individually held animals and Amur leopards paced the most, but because stereotypic behaviours are individually developed and expressed it is difficult to generalise with this few animals observed. Research has shown that pacing in felids is often caused by unavoidable stress or fear (Mason *et al*. 2007). Factors such as small night holdings (Mallapur and Cheelam, 2002), visitor density (Sellinger & Ha 2005), being housed near natural predators (Carlstead *et al*. 1993), lack of access to hiding places (Fanson & Wielebnowski 2013) and starving days (Lyons *et al*. 1997) affect development and level of stereotypic behaviours.

Mason *et al* (2007) list three reasons for animals to develop stereotypical behaviours; (1) the animal's internal state evoked by the environment, sometimes in combination with external cues, (2) environmentally induced chronic stress affecting the brain and internal motivation chains, and (3) environmental conditions during rearing has damaged the development of the central nerve system. Stereotypic behaviours might help the animal to alleviate negative emotions (Mason *et al* 2007), but even so it is a sign of poor welfare. It might be triggered by keepers' presence, hunger etc., and it could be a fixed pattern or damage from infanthood. Whatever the cause it is important to investigate the situation and behaviours of each animal to make sure not to miss any risk of poor welfare.

5.3.2 Use of resources

The felids in this study used some kind of resource in their enclosures 42 % of the observed time. The most used resources were elevated resting or perching places such as for instance a cliff ledge, on top of a hut, a platform or a climbing tree (Figure 5). This result supports the findings of Mallapur *et al*. (2002) and Lyons *et al*. (1997). In accordance with the findings of Fanson & Wielebnowski (2013) the usage of hiding places or covered resting places was also considerable. For females the difference between use of elevated resting places and being within a hiding place were less than for males (Figure 5). This might be not so much a sex difference as an effect of motherhood. One quarter of the studied females had kittens or cubs which might have affected their behaviour into more hiding than normally. Both the female Pallas's cat at Nordens Ark and her kittens changed hiding place frequently showing the importance to provide optional nesting boxes as stated in the Pallas's cat husbandry guidelines (Barclay 2013).

Amur leopards chose elevated resources over hiding place almost every time (Figure 6). Persian leopards and snow leopards also preferred elevated resources but were observed within shelters as well (Figure 6). Tigers equally used both elevated resources and huts for resting (Figure 6). Cheetahs were mostly on the ground and Pallas's cats within hiding places (Figure 6). These differences could be explained by natural differences in ecology and evolution but since the study sample is small it might also be an expression of individuality and enclosure design.

Even though the habitats where these felids live in the wild vary both within populations and individual home ranges there are some basic differences which might reflect the felids' behaviours. Cheetahs mostly live in savannahs or bushlands with open views of the surroundings in contrast to tigers which live in more dense forested areas (Broomhall *et al*. 2004, Carroll & Miquelle 2006, Linkie *et al*. 2006). Leopards are found in a wide range of habitats but are often resting, eating or hiding prey in trees to avoid competition from other carnivores (Sunquist & Sunquist 2002). Tigers are top predators and as such can afford to be more relaxed when choosing a resting place (Carroll & Miquelle 2006, Linkie *et al*. 2006). The Pallas's cat's vulnerability to be killed by larger predators such as lynx or snow leopards (Donadio & Buskirk 2006), as discussed above, might motivate a stronger preference for hiding places in daytime than with the other observed species in this study.

The cheetahs at Parken Zoo were lying in the grass in the back end of the enclosure even though they had access to a hut and a hill. The hut was in the front end of the enclosure and it was only possible to be inside and not on top of it. The hill, although offering elevated viewing, was covered with high vegetation which possibly prevented them from overview or maybe was uncomfortable. It is hard to know whether the cheetahs chose their resting spot because of its location away from visitors, with a view over alpacas and ostriches, or because the available alternative resources were not suitable.

5.3.3 Use of enclosures

All species except the Sumatran tigers, but not all enclosures, were designed with areas distinctly elevated above other parts of the enclosure and the public viewing points. The individuals which had access to elevated areas in their enclosures used these for about 22 % of the time they were seen (Figure 9). This level is very likely higher because in several out of sight-markings the individuals probably were hiding in elevated areas as they had been seen there before or after observations. Interestingly the snow leopards at Nordens Ark, which have a large enclosure with a high cliff, still choose the lower areas the majority of the time. Socially held animals used the elevated areas least but the usage varied greatly within this group (Figure 9).

The number of zone changes varied individually as well as over time but males had a higher mean number of zone changes than females (Figure 10). Male felids mostly have larger home ranges than females and often overlapping several females' home ranges (e.g. Sliwa 2004, Benson *et al*. 2006, Carroll & Miquelle 2006; Linkie *et al*. 2006, Cascelli de Azevedo & Murray 2007). To mark his home range and defend his access to the females in his range the male cover larger areas and move around more. Species differences in number of zone changes (Figure 10) are in this study most probably too compromised by a small number of individuals to allow any general conclusions.

Enclosure usage is depending on design and layout of each enclosure. All individuals had favourite places where they were observed a majority of the observed time. The Persian leopard at Orsa rovdjurspark is the only exception because he was observed patrolling the whole range of his enclosure the majority of the time, and the few times he did rest the resting places varied from time to time. Each individual had one or a few favourite spots which all of them were resting places. The socially held felids sometimes shared resting place but also alternated in using the same spot.

Both Mallapur & Chellam (2002) and Sellinger & Ha (2005) found that visitor density and visitor intensity affected behaviours such as hiding and pacing. At Orsa rovdjurspark the visitors could walk around almost all of the Persian leopards' and snow leopards' enclosures. Three of the four individuals were to a very high degree passive, both females hiding either indoors or in the central part of the enclosure, and the snow leopard male lying on top of a platform in the middle of the enclosure. By this the animals were placing themselves as far away from the visitors as possible.

The two larger Amur tiger enclosures at Nordens Ark were large naturalistic enclosures with a high cliff in the middle where the animals were more or less unseen by the visitors. Yet especially the older male preferred to be in the very small cage lock resting on top of the hut. The cage locks are located in an area not accessible to the public but so is also approximately half of the enclosure. The female was pacing when kept in the small enclosure but not in the medium sized one, indicating she preferred the larger area. Whether her pacing was invoked by the enclosure size or the proximity to people could not be determined.

The two most pacing individuals, the female Amur leopard at Nordens Ark and the male Amur tiger at Orsa rovdjurspark, were doing this along the fence very close to the visitors. This was also either as close to or far away from the other sex in the neighbouring enclosure as possible. It could not be determined whether it was the proximity/distance to the other sex, or visitors or just that it was the perimeter of the enclosure that determined where the individual chose to pace.

The female cheetah with cubs often used the area with the hut but it is hard to distinguish whether it was the safety from the rhinoceroses or the hut itself that motivated her choice.

Overview or cover are important for the felids but other factors might also be important for choice of resting place, such as soft grass or bedding, the materials ability to retain warmth or cold, weather sheltering, neighbouring species and distance to visitors. All this needs to be taken into account when designing enclosures for the felids.

5.4 Notes about the study and further research

In order to increase the study sample this study was performed in four zoos and each felid species was represented in at least two of these zoos. But even so, the number of individuals was low which made it difficult to generalise the results, especially on species level.

Data about weather conditions and visitor density was noted for each session but was tested with a linear regression analysis and found to have no impact on the result in this study and was therefore left without further discussion.

The most evident result of this study is that it is not easy to distinguish why felids prefer one resource or type of enclosure to another, or which factors are most important for the felids. To ensure optimal felid welfare it would be of interest to perform preference studies over a longer time and larger sample size.

Because felids are crepuscular and nocturnal and therefore mostly active from dusk to dawn (Sunquist & Sunquist 2002) it is important to know the behaviours of the zoo kept felids also during the nights and how they use their resources and enclosure when no humans are present. It would be possible to perform both behavioural studies and preference tests with the help of night vision cameras and video recordings.

We need to study not only the effects of different enrichments in order to decrease stereotypic behaviours and suboptimal welfare, but which enclosures and resources the different felids need and prefer in order to have an optimal welfare. We also need to find out the circumstances where stereotypes are developed and may become fixed behaviours in order to understand what impact the stereotypic behaviours have on the felids welfare.

In further research we also need to replace the small one-institutional behavioural studies with multi-institutional studies with large number of individuals of all zoo kept felid species. Research with large study samples where the results can be generalised, covering not just the large felid species but also the smaller ones. Even though felids in many ways are similar, there are species differences and we need to find out which behavioural differences are important to welfare.

5.5 Ethical reasoning

Should we keep felids in zoos at all? They are difficult to maintain without welfare problems (e.g. Mason & Latham 2004, Hope & Deem 2006, Mason 2010). They are expensive to keep as they need vast areas and advanced security measures. They are also mostly inactive during opening hours and often hide from the zoo visitors (Turnock & Moss 2015), making them a suboptimal exhibit.

Felids are intriguing majestic animals that are hard to experience in the wild. Research done in zoos might contribute to better understanding of the elusive wild felids (Romano *et al*. 2010). In zoos we have the opportunity to come close and to study them, but is that enough of a reason to keep felids in captivity when there are so many welfare problems?

Because felids are popular with the public they are good ambassadors for teaching about environmental problems and conservation efforts (Moss & Esson 2010, 2013). On the other hand, visitors react negatively upon seeing animals perform stereotypical behaviours (Miller 2012).

Due to an expanding human population there are more and more conflicts between felids and humans and many of the felid species are threatened with extinction (Zanin *et al*. 2015). One can argue that because it is humans causing the decline we are responsible to try to save these animals. Since there are not enough habitat areas and often very small gene pools in the wild we need to keep them in zoos and maintain a viable population while waiting for better conditions in the wild (Henry *et al*. 2009, Penfold *et al*. 2014). We do not know if that will ever happen, or if the zoo felids will still be able to function in the wild when that time comes.

If we are to keep felids in zoos and try to maintain a healthy population for both information and conservation purposes we need to keep them with optimal welfare. If they are to function as ambassadors for conservation work they must attract the visitors, they must be visible but at the same time show natural behaviours instead of stereotypes. We must therefore be able to provide the zoo felids with the right type of enclosure designs and resources important to their welfare. To be able to accomplish that it is important that the research done in this area is performed on a larger scale to give us proper scientific knowledge about what they need.

5.6 Conclusions

None of the reviewed articles looked into which of different resources in the enclosure the animals preferred. Studies on which resources felids need, and if these differ between species, are missing.

There seems to be a gap in communication between recent scientific research and zoo husbandry. Zoo husbandry practices are therefore probably based mainly on traditions and anecdotal knowledge.

Except for minor differences felids behave similarly regardless of species but they have individual preferences. It is therefore important to evaluate each individual when designing social or individual holding.

Providing several elevated resting places in the back end of the enclosure might enable both increased welfare and visible animals for the visitors.

Numerous hiding places where the felids can avoid both conspecifics and visitors are important, especially for the smaller felid species, but other factors than overview or cover might also be important for choice of resting place.

In future research we need to replace the small one-institutional behavioural studies with multi-institutional studies with large number of individuals of all zoo kept felid species.

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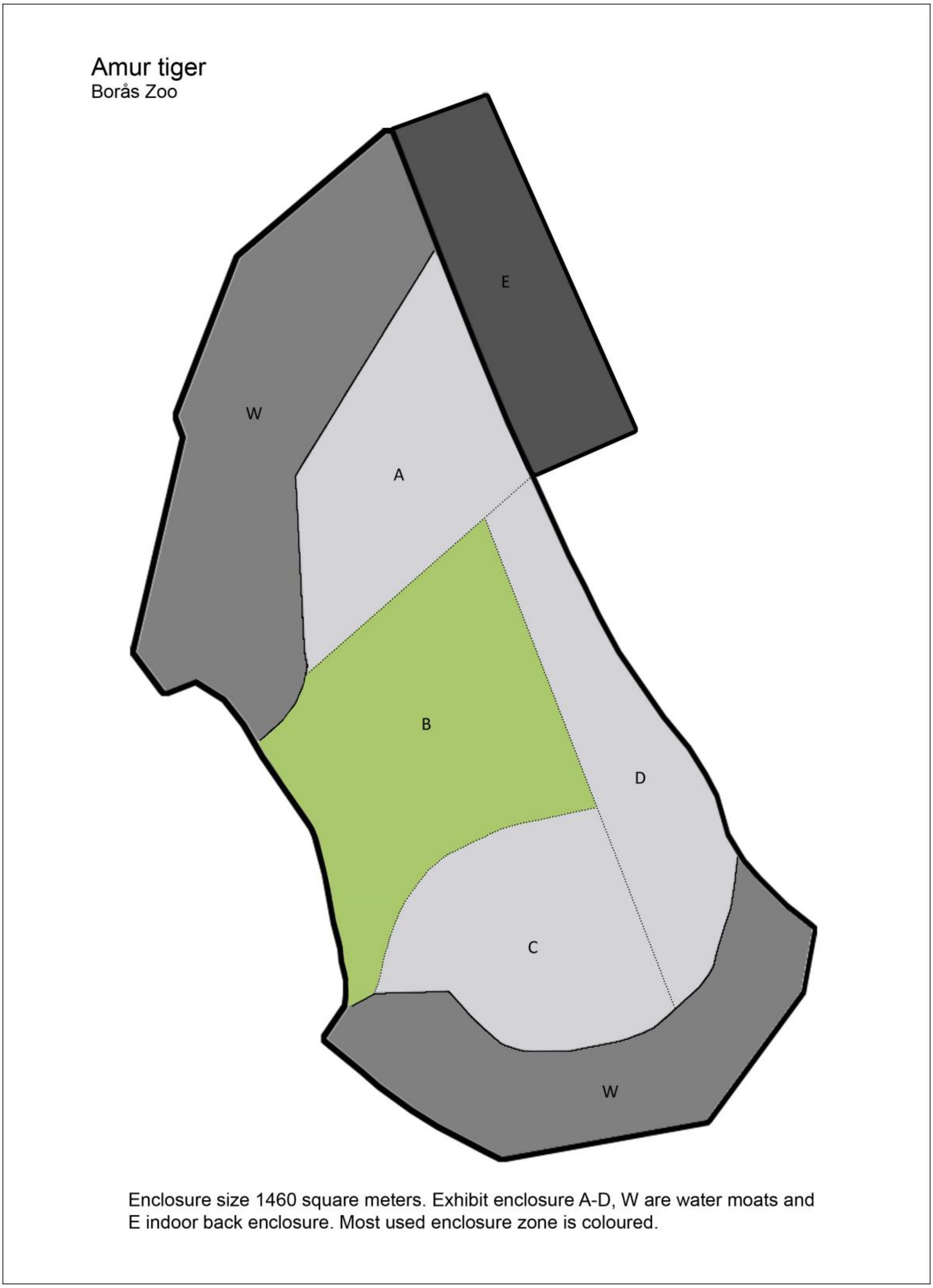
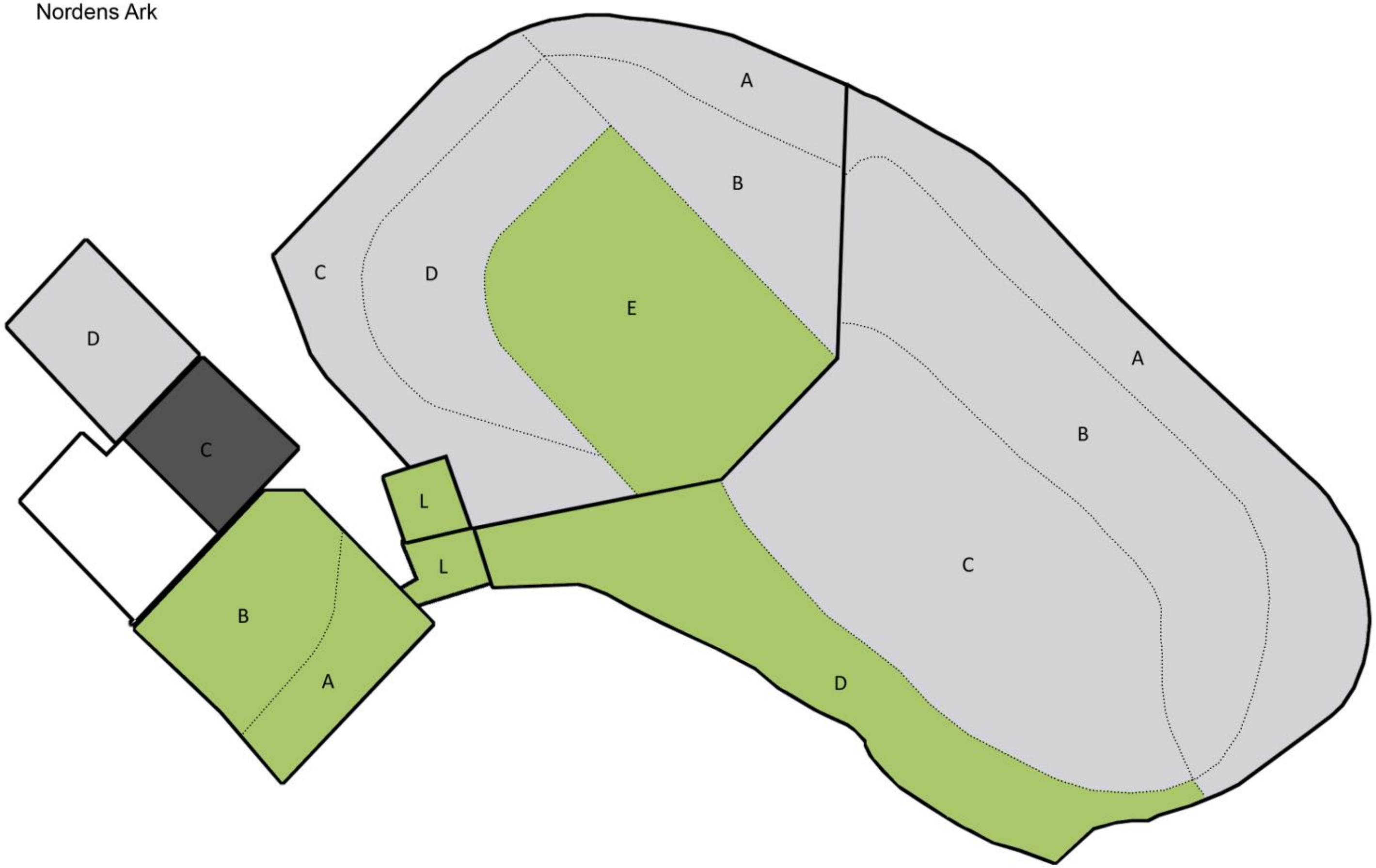
8 Appendixes

8.1 Appendix 1 Enclosure maps

Note that the maps are not to scale with each other.



Amur tiger
Nordens Ark



All tigers are rotated between three enclosures, the large exhibit enclosure to the right (~3500 sq.m.), the medium exhibit enclosure in the middle (~2500 sq.m.) and the small enclosure to the left comprising the exhibit area, the indoor area and the back area (~500 sq.m). Two cage locks (L) connects the three exhibit enclosures. Most used zones in each enclosure are coloured.

Amur tiger
Orsa rovdjurspark

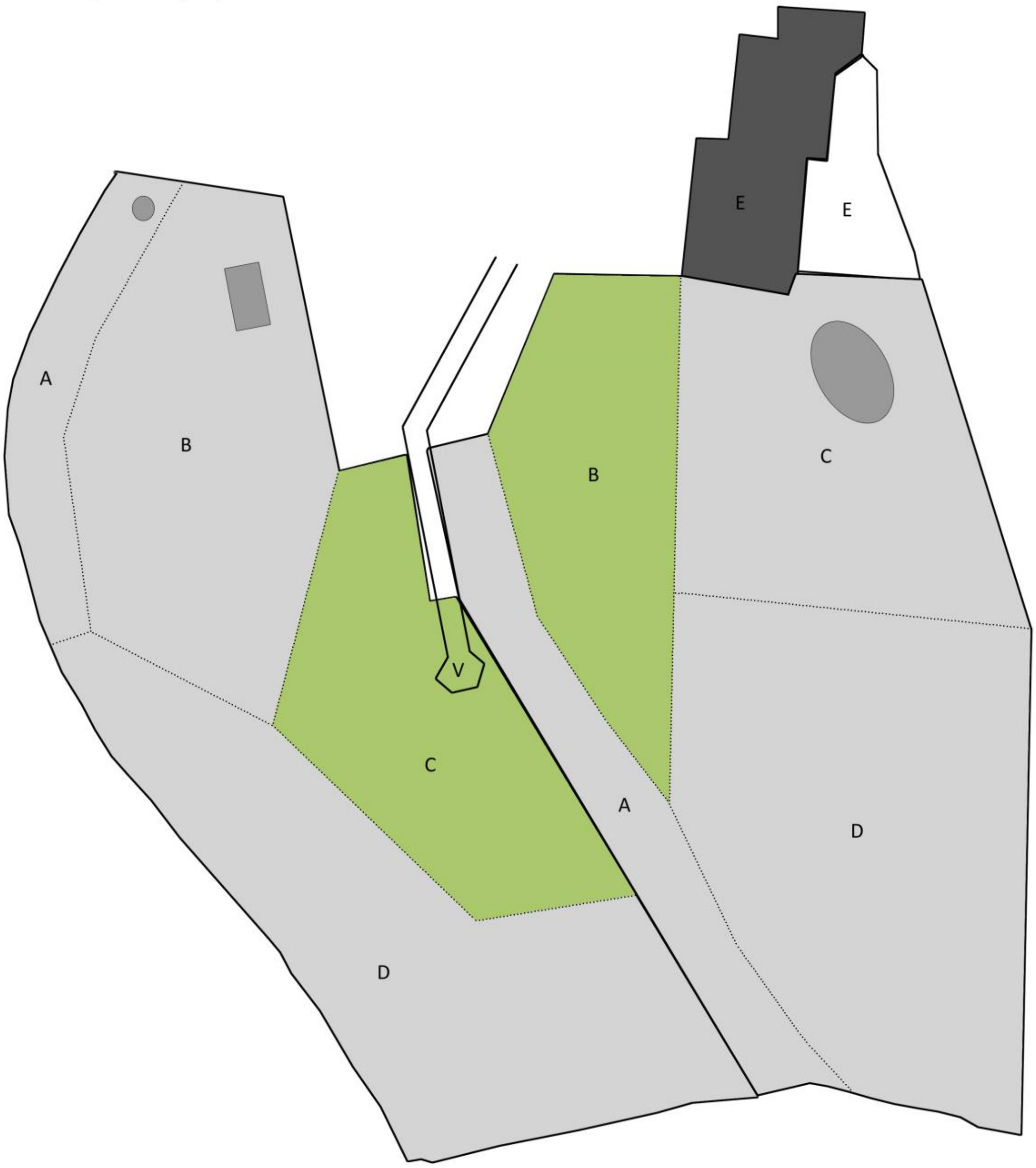
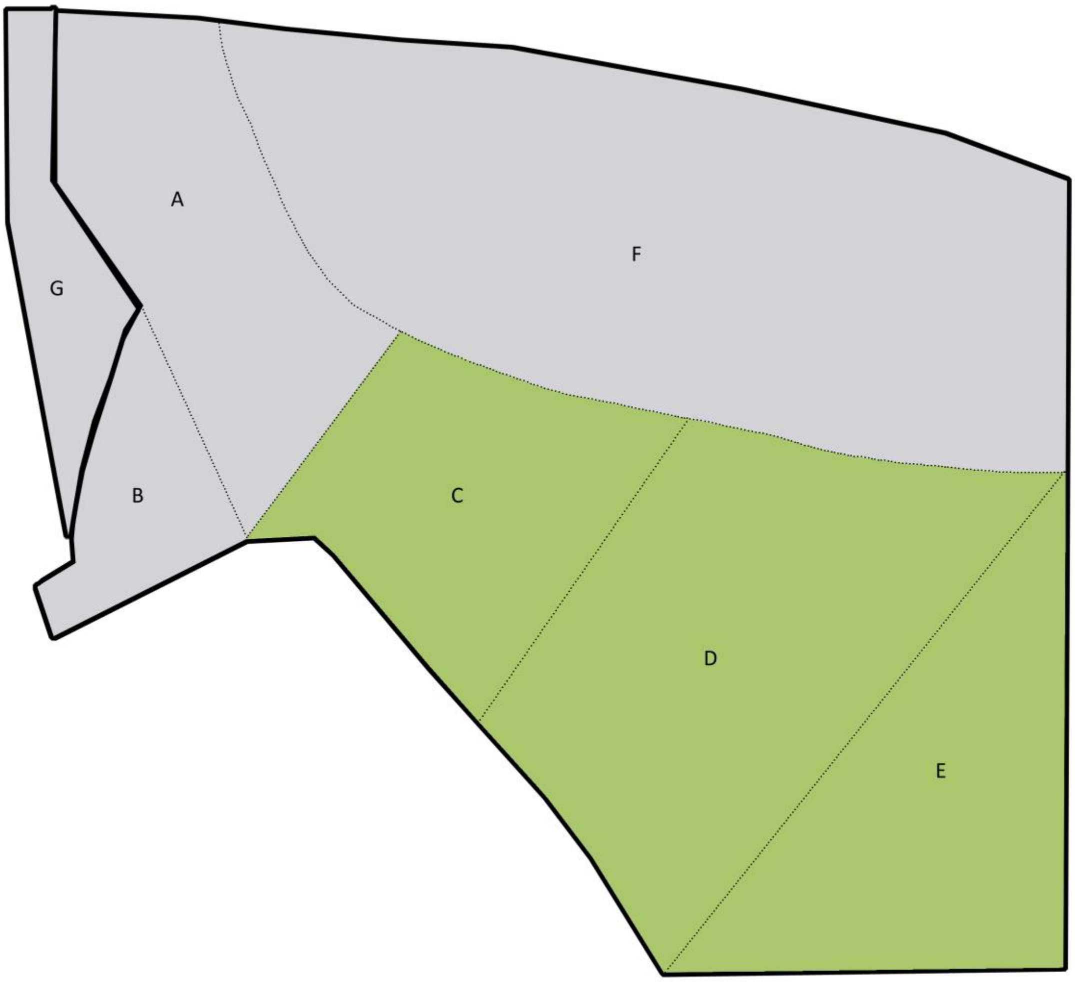


Exhibit enclosures 14000 square meters. Male enclosure to the left, female enclosure to the right. E are back (150 sq.m.) and indoor (340 sq.m.) enclosures. V is a visitor bridge above the enclosures.
Most used zone in each enclosure is coloured.

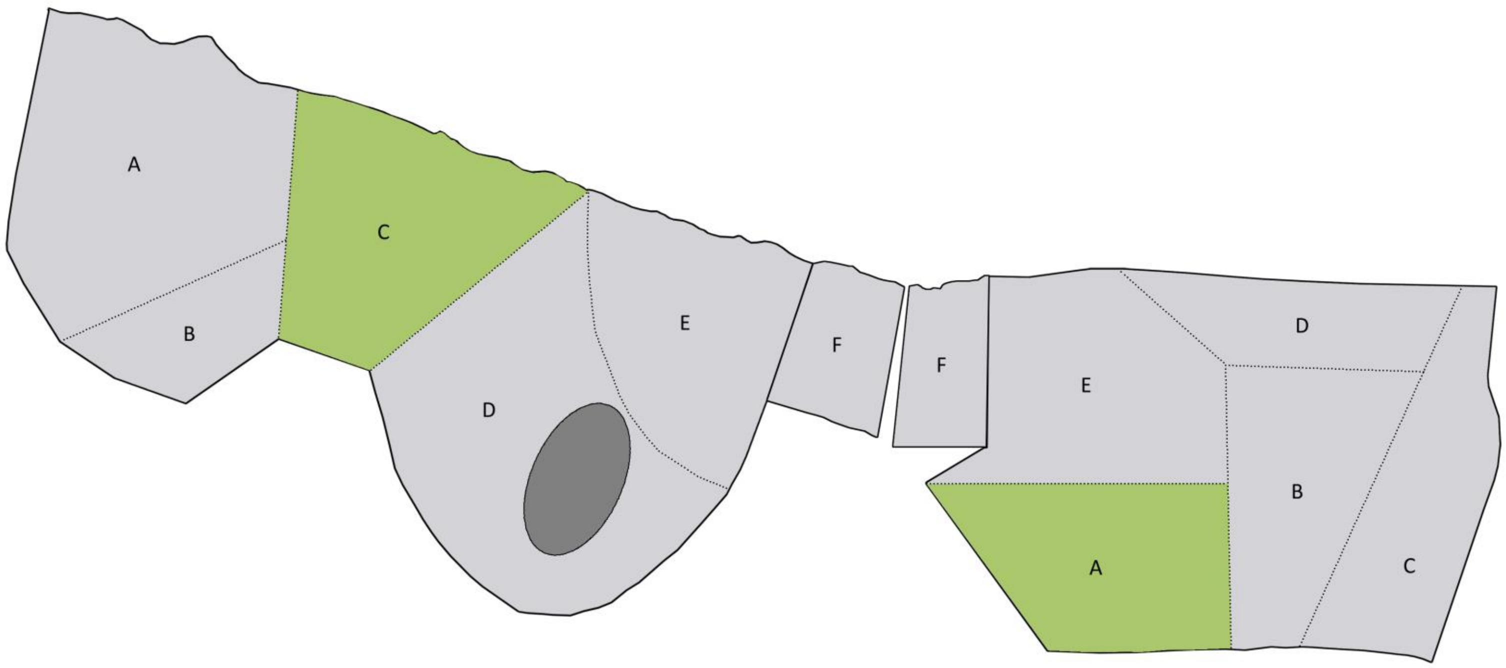
Sumatran tiger
Parken Zoo



Enclosure size 3560 square meters. Exhibit enclosure A-F, back enclosure G.
Most used enclosure zones are coloured.

Amur leopard

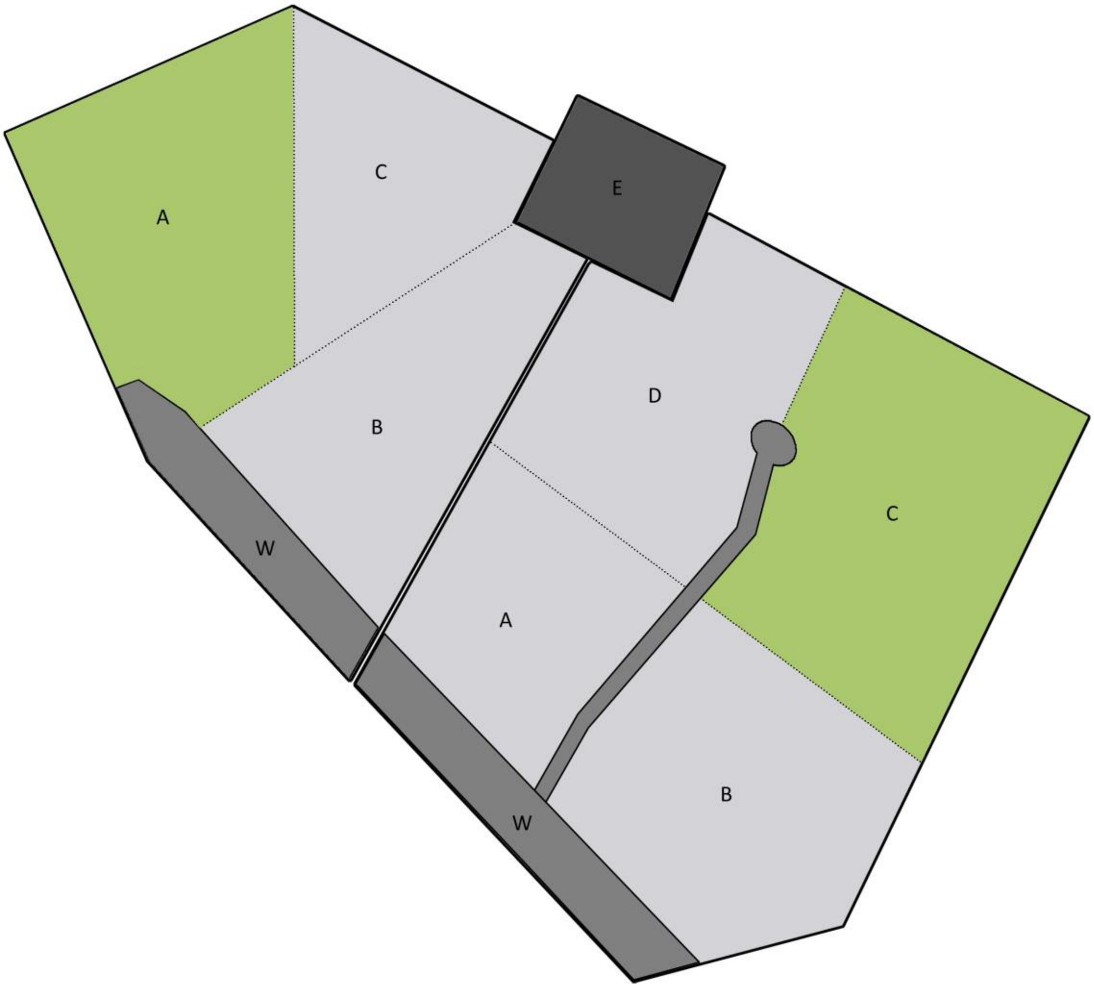
Nordens Ark



Male enclosure to the left (670 sq.m.), female enclosure to the right (540 sq.m.). F are back enclosures.
Most used zone in each enclosure is coloured.

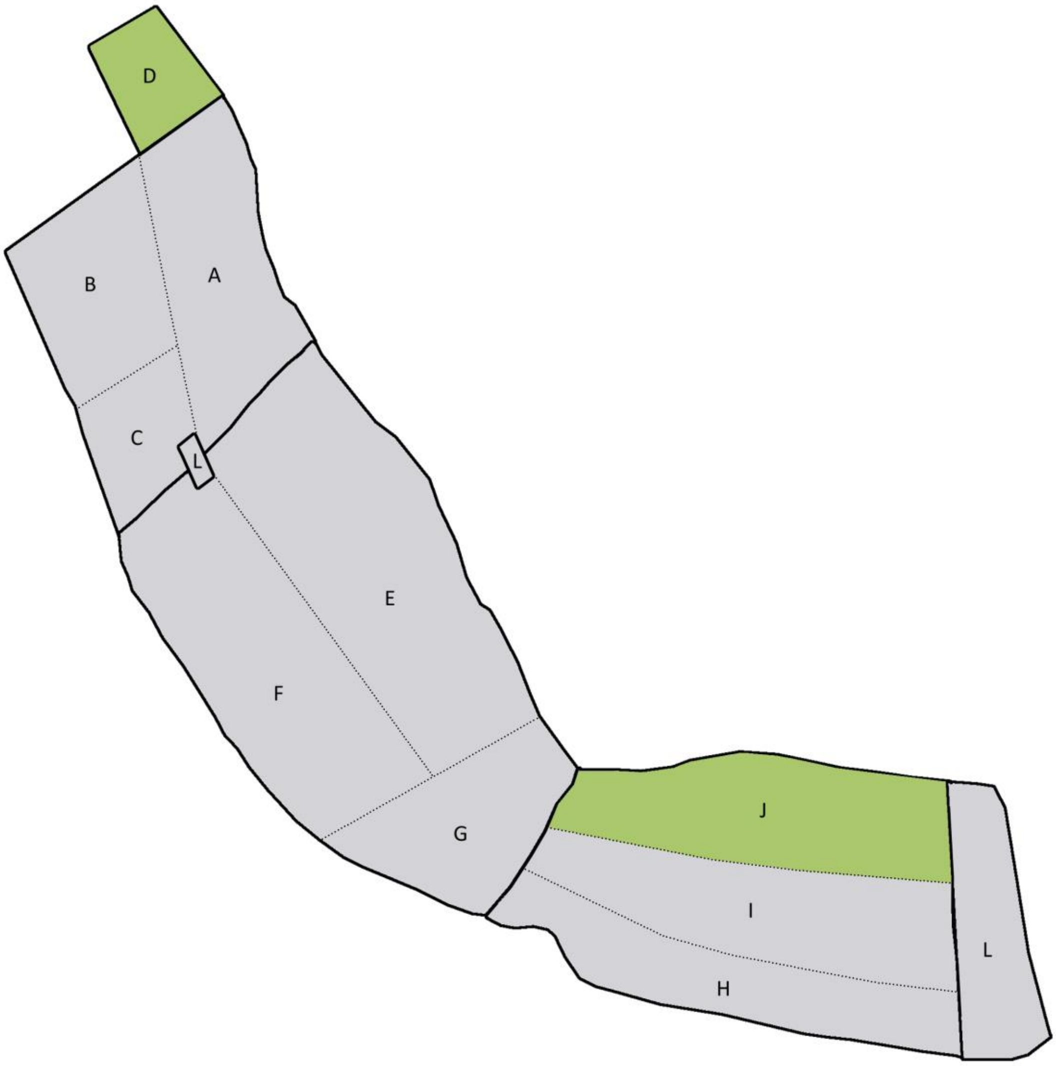
Amur leopard

Parken Zoo



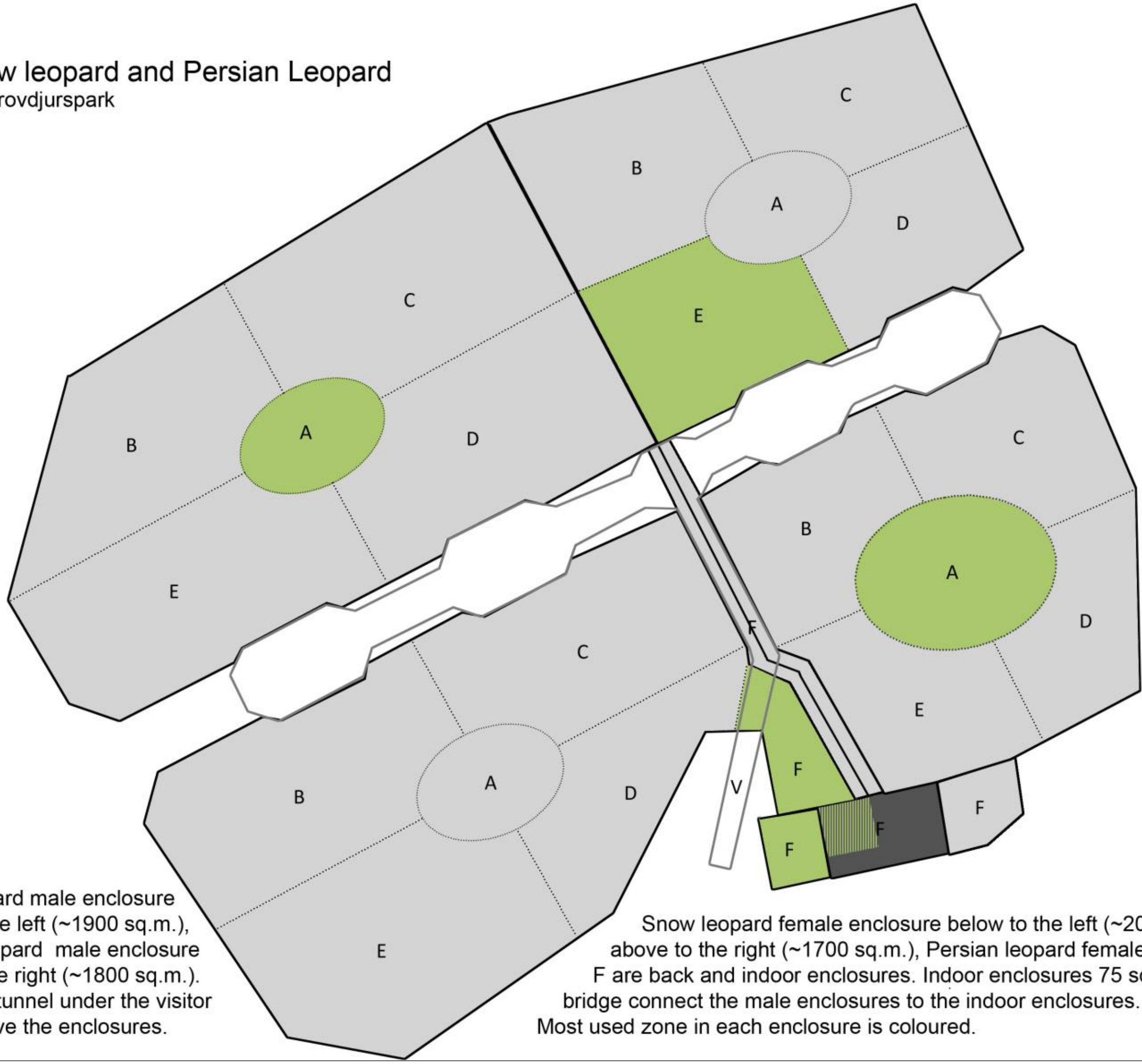
Female enclosure to the left (550 sq.m)., male enclosure to the right (800 sq.m.).
W are water moats and E is indoor back enclosure.
Most used zone in each enclosure is coloured.

Persian leopard
Nordens Ark



Enclosure size 2100 square meters. Three exhibit enclosures connected with each other. Three cage locks (D and L) although the cage lock to the right was temporary closed off.
Most used enclosure zones are coloured.

Snow leopard and Persian Leopard
Orsa rovdjurspark

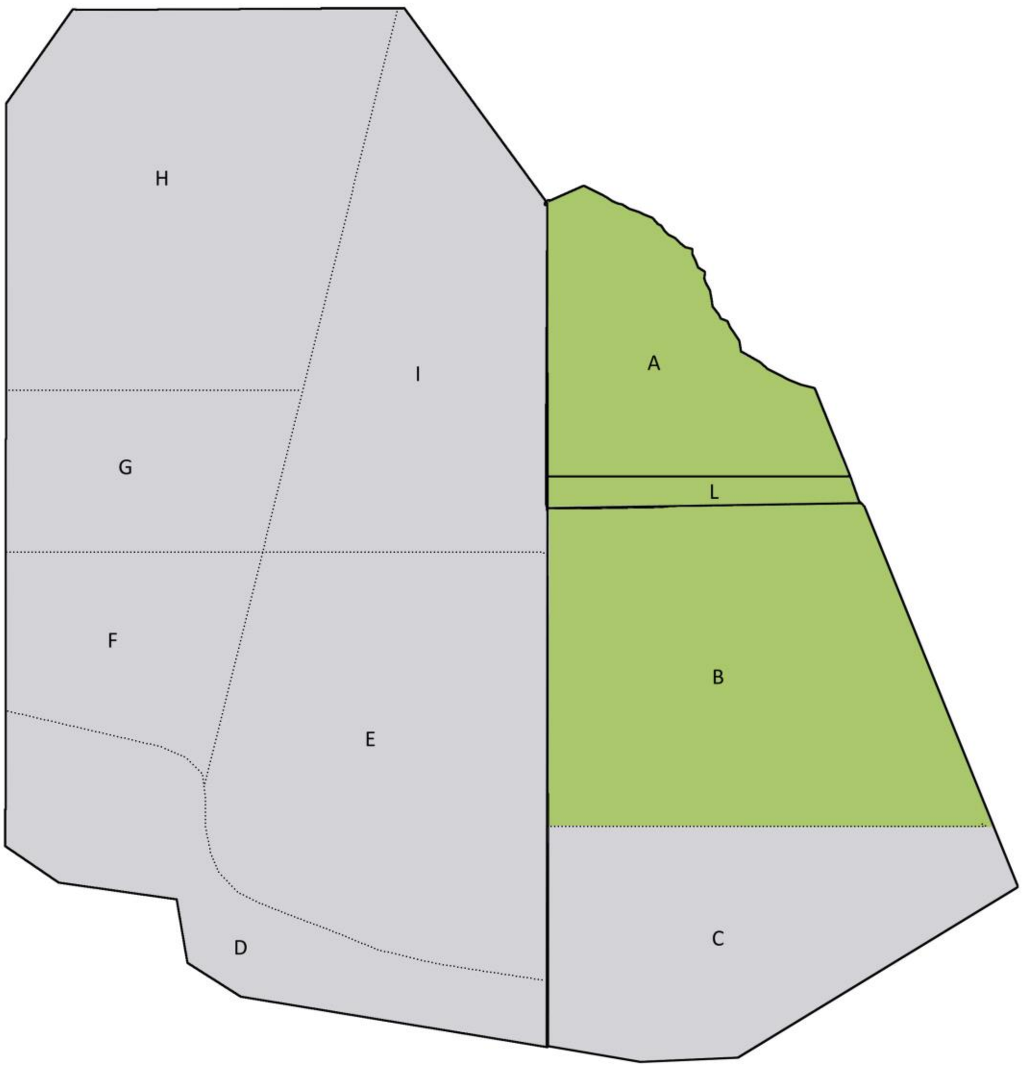


Snow leopard male enclosure above to the left (~1900 sq.m.), Persian leopard male enclosure below to the right (~1800 sq.m.). species. A tunnel under the visitor bridge above the enclosures.

Snow leopard female enclosure below to the left (~2000 sq.m.). above to the right (~1700 sq.m.), Persian leopard female enclosure F are back and indoor enclosures. Indoor enclosures 75 sq.m. per bridge connect the male enclosures to the indoor enclosures. V is a visitor Most used zone in each enclosure is coloured.

Snow leopard

Nordens Ark



Enclosure size 1950 square meters. Three exhibit enclosures connected with each other. One cage lock (L) where the snow leopards often lie on top of the mesh roof. Most used enclosure zones are coloured.

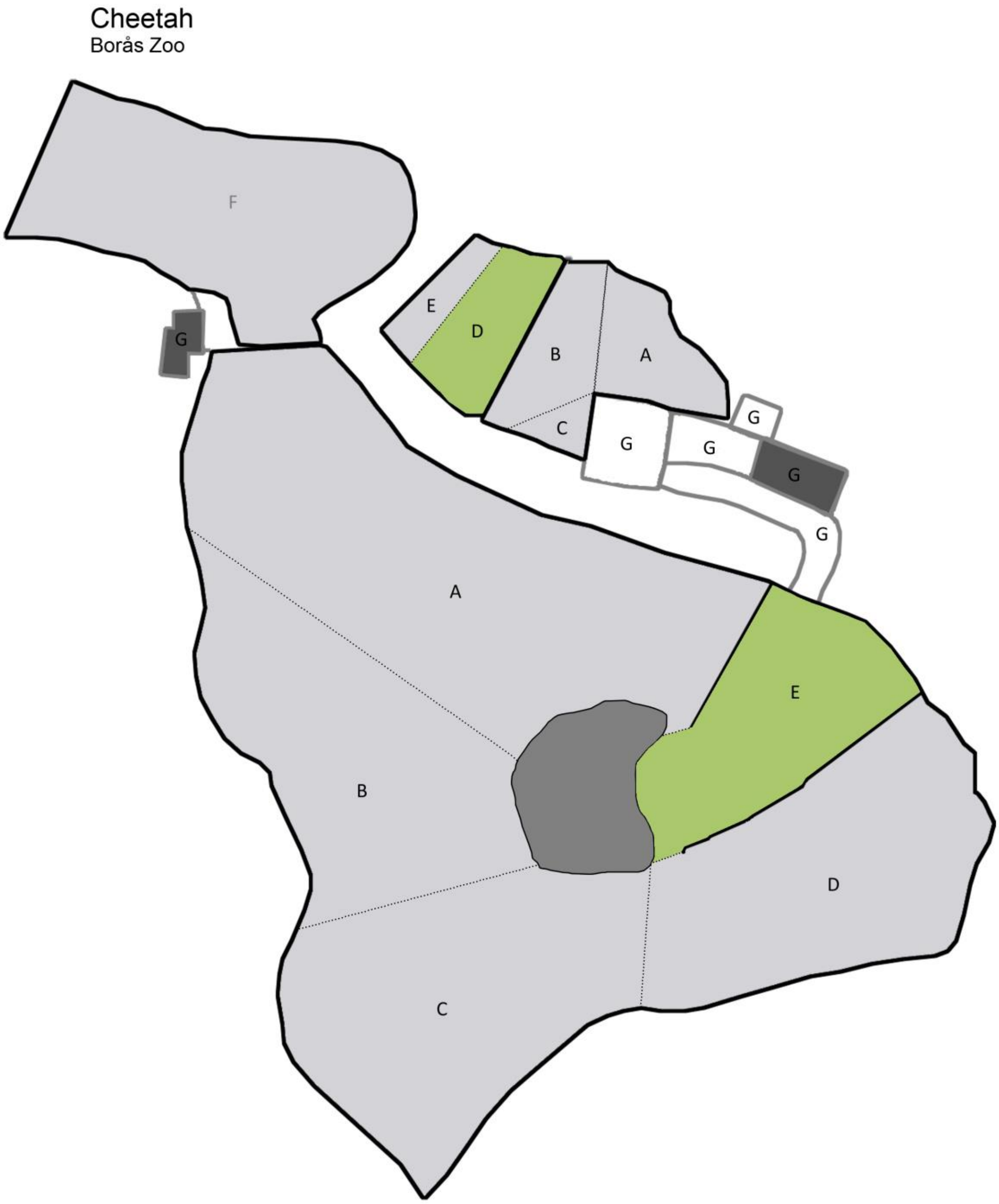
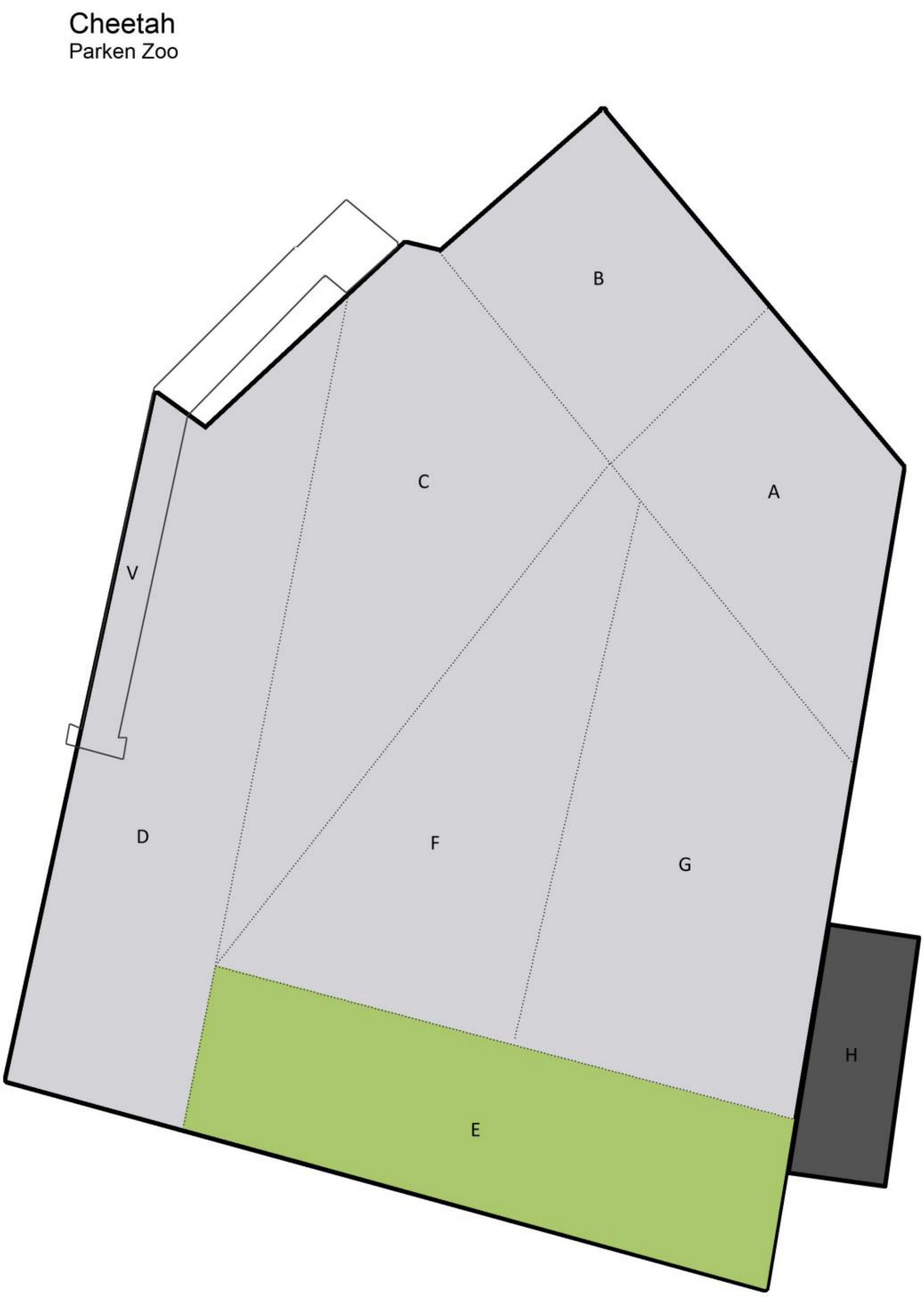
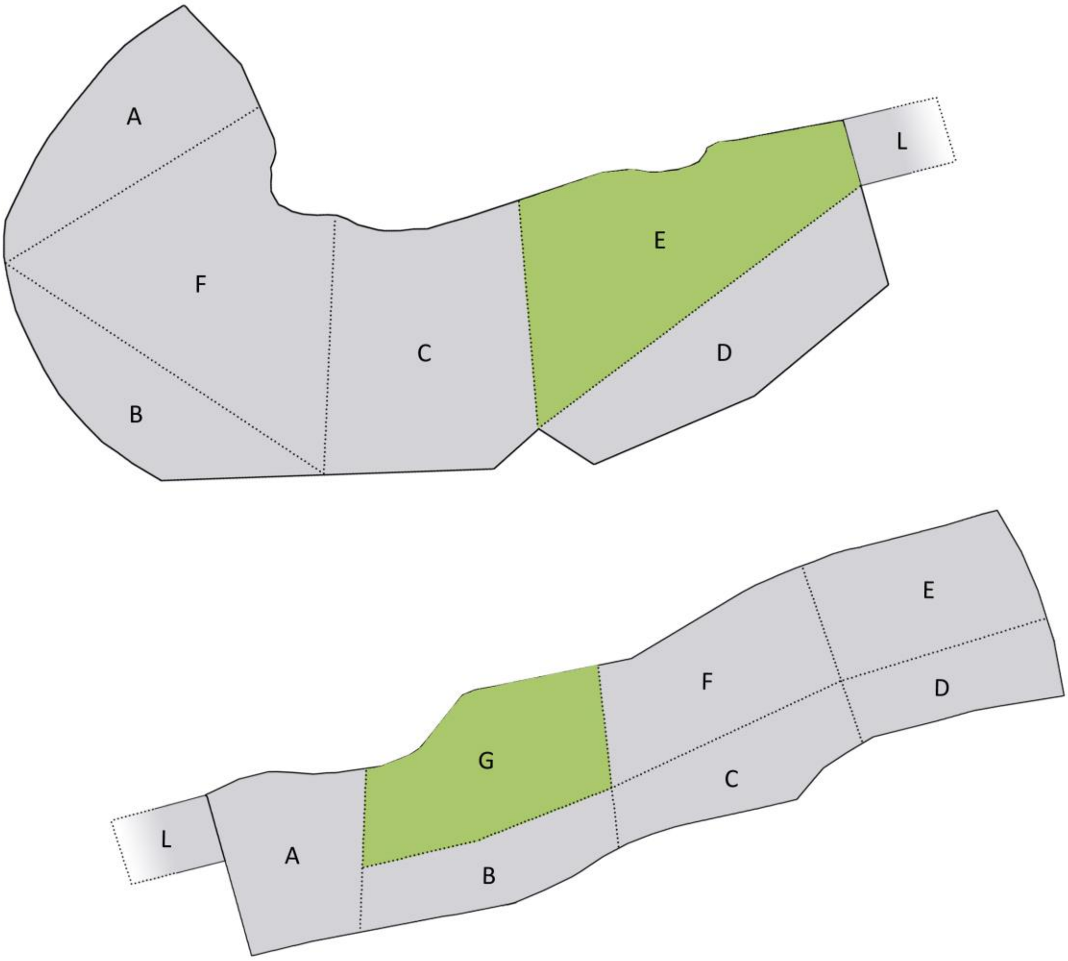


Exhibit enclosure A-E below (6700 sq.m.), studied back enclosure A-E above (540 sq.m.). Exhibit enclosure A-D is shared by cheetahs and rhrhinoceros, area E is protected from the rhinoceros. F is rhinoceros back enclosure and G are back and indoor enclosures not included in the study. Most used zone in each enclosure included in the study is coloured.



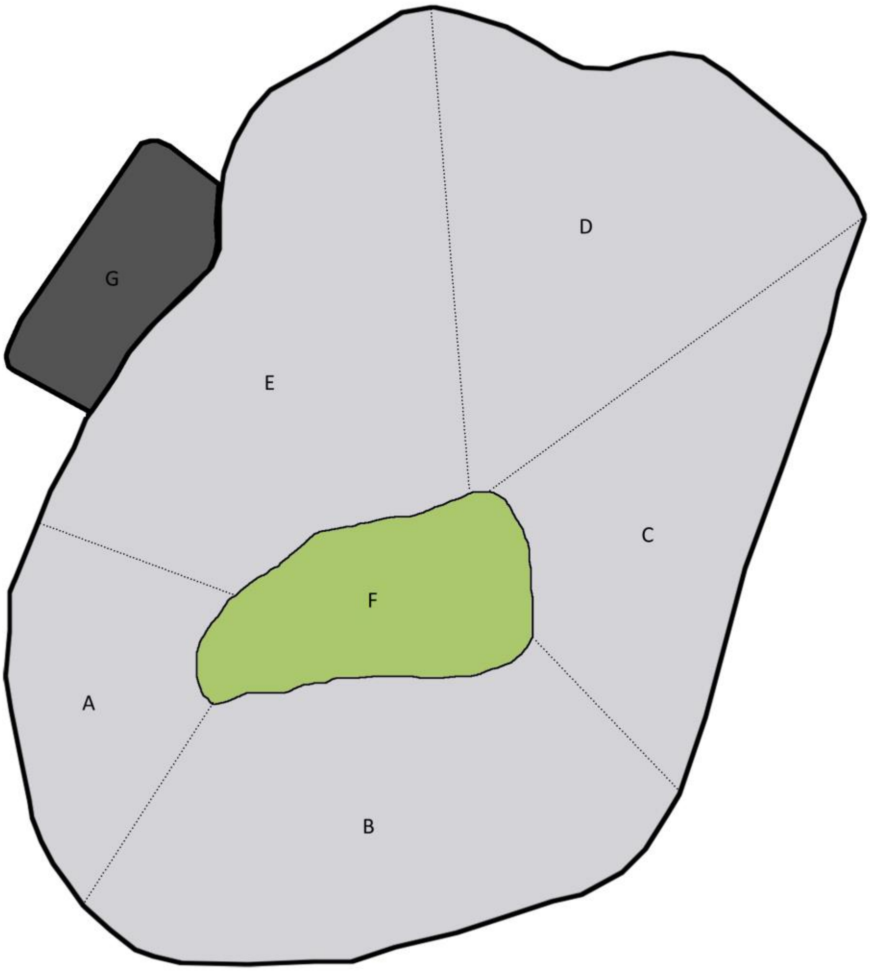
Enclosure size 3080 square meters. Exhibit enclosure A-G. H is indoor back enclosure (82 sq.m.) and V is a visitor bridge above the enclosure. Most used enclosure zone is coloured.

Pallas's cat
Nordens Ark



Female enclosure to the left, 300 sq.m. (above), male enclosure to the right 300 sq.m. (below). A cage lock (L) connects the two enclosures.
Most used zone in each enclosure is coloured.

Pallas's cat
Parken Zoo



Enclosure size 390 square meters.Exhibit enclosure A-F. G is indoor back enclosure.
Most used enclosure zone is coloured.

8.2 Appendix 2 Literature review articles

8.2.1 Reviewed articles

Barja I & de Miguel FJ (2010) Chemical communication in large carnivores: Urine-marking frequencies in captive tigers and lions. Polish Journal of Ecology 58, 397-400

Bashaw MJ, Kelling AS, Bloomsmith MA & Maple TL (2007) Environmental effects on the behavior of zoo-housed lions and tigers, with a case study of the effects of a visual barrier on pacing. Journal of Applied Animal Welfare Science 10, 95-109

Breton G & Barrot S (2014) Influence of enclosure size on the distances covered and paced by captive tigers (*Panthera tigris*). Applied Animal Behaviour Science 154, 66–75

Burgener N, Gusset M & Schmid H (2008) Frustrated Appetitive Foraging Behavior, Stereotypic Pacing, and Fecal Glucocorticoid Levels in Snow Leopards (*Uncia uncia*) in the Zurich Zoo. Journal of Applied Animal Welfare Science 11, 74-83

Castillo-Guevara C, Unda-Harp K, Lara C & Serio-Silva JC (2012) Enriquecimiento Ambiental y su Efecto en la Exhibición de Comportamientos Esterotipados en Jaguares (*Panthera onca*) del Parque Zoológico "Yaguar Xoo", Oaxaca. Acta Zoológica Mexicana 28, 365-377 (in Spanish, abstract in English)

Chadwick CL, Rees PA & Stevens-Wood B (2013) Captive-Housed Male Cheetahs (*Acinonyx jubatus soemmeringii*) Form Naturalistic Coalitions: Measuring Associations and Calculating Chance Encounters. Zoo Biology 32, 518-527

Chosy J, Wilson M & Santymire R (2014) Behavioral and Physiological Responses in Felids to Exhibit Construction. Zoo Biology 33, 267-274

Clubb R, & Mason GJ (2007) Natural behavioural biology as a risk factor in carnivore welfare: How analysing species differences could help zoos improve enclosures. Applied Animal Behaviour Science 102, 303-328

De Rouck M, Kitchener AC, Law G & Nelissen M (2005) A comparative study of the influence of social housing conditions on the behaviour of captive tigers (*Panthera tigris*). Animal Welfare 14, 229-238

DeCaluwea HB, Wielebnowski NC, Howard J, Pelican KM & Ottinger MA (2013) Behavioral reactions relate to adrenal activity and temperament in male clouded leopards (*Neofelis nebulosa*). Applied Animal Behaviour Science 149, 63–71

Fanson KV & Wielebnowski NC (2013) Effect of housing and husbandry practices on adrenocortical activity in captive Canada lynx (*Lynx canadensis*). Animal Welfare. 22 159-165

Gartner MC & Powell D (2012) Personality assessment in snow leopards (*Uncia uncia*). Zoo Biology 31, 151-165

Kelling AS, Allard SM, Kelling NJ, Sandhaus EA & Maple TL (2012) Lion, Ungulate, and Visitor Reactions to Playbacks of Lion Roars at Zoo Atlanta. Journal of Applied Animal Welfare Science 15, 313-328

Macri AM & Patterson-Kane E (2011) Behavioural analysis of solitary versus socially housed snow leopards (*Panthera uncia*), with the provision of simulated social contact. Applied Animal Behaviour Science 130, 115-123

Margulis SW, Hoyos C & Anderson M (2003) Effect of felid activity on zoo visitor interest. Zoo Biology 22, 587–599

Martínez-Macipe M, Lafont-Lecuelle C, Manteca X, Pageat P & Cozzi A (2015) Evaluation of an innovative approach for sensory enrichment in zoos: semiochemical stimulation for captive lions (*Panthera leo*). Animal Welfare 24, 455-461

Miller LJ, Bettinger T & Mellen J (2008) The reduction of stereotypic pacing in tigers (*Panthera tigris*) by obstructing the view of neighbouring individuals. Animal Welfare 17, 255–258

Miller A, Leighty KA, Maloney MA, Kuhar CW & Bettinger TL (2011) How access to exhibit space impacts the behavior of female tigers (*Panthera tigris*). Zoo Biology 30, 479–486

Miller A, Leighty KA & Bettinger TL (2013) Behavioral analysis of tiger night housing practices. Zoo Biology 32, 189-194

Mohapatra RK, Panda S & Acharya UR (2014) Study on activity pattern and incidence of stereotypic behavior in captive tigers. Journal of Veterinary Behavior-Clinical Applications and Research 9, 172-176

Mollá MI, Quevedo MA & Castro F (2011) Bobcat (*Lynx rufus*) Breeding in Captivity: The Importance of Environmental Enrichment. Journal of Applied Animal Welfare Science 14, 85-95

Moreira N, Brown JL, Moraes W, Swanson WF & Monteiro-Filho ELA (2007) Effect of housing and environmental enrichment on adrenocortical activity, Behavior and reproductive Cyclicity in the female tigrina (*Leopardus tigrinus*) and margay (*Leopardus wiedii*). Zoo Biology 26, 441-460

Quirke T & O' Riordan RM (2011a) The effect of different types of enrichment on the behaviour of cheetahs (*Acinonyx jubatus*) in captivity. Applied Animal Behaviour Science 133, 87–94

Quirke T & O' Riordan RM (2011b) The effect of a randomised enrichment treatment schedule on the behaviour of cheetahs (*Acinonyx jubatus*). Applied Animal Behaviour Science 135, 103-109

Quirke T & O' Riordan RM (2015) An Investigation into the Prevalence of Exploratory Behavior in Captive Cheetahs (*Acinonyx jubatus*). Zoo Biology 34, 130–138

Quirke T & O' Riordan RM & Zuurb A (2012) Factors influencing the prevalence of stereotypical behaviour in captive cheetahs (*Acinonyx jubatus*). Applied Animal Behaviour Science 142, 189–197

Quirke T, O' Riordan RM. & Davenport J (2013) A Comparative Study of the Speeds Attained by Captive Cheetahs during the Enrichment Practice of the "Cheetah Run". Zoo Biology 32, 490-496

Resende LS, Remy GL, de Almeida Ramos Jr V & Andriolo A (2009) The influence of feeding enrichment on the behavior of small felids (*Carnivora: Felidae*) in captivity. Zoologica 26, 601-605

Resende LS, Pedretti Gomes KC, Andriolo A, Genaro G, Remy GL & de Almeida Ramos Jr V (2011) Influence of Cinnamon and Catnip on the Stereotypical Pacing of Oncilla Cats (*Leopardus tigrinus*) in Captivity. Journal of Applied Animal Welfare Science 14, 247-254

Resende LS, Neto GL, Carvalho PGD, Remy GL, de Almeida Ramos Jr V, Andriolo A & Genaro G (2014). Time Budget and Activity Patterns of Oncilla Cats (*Leopardus tigrinus*) in Captivity. Journal of Applied Animal Welfare Science 17, 73-81

Romano MC, Rodas AZ, Valdez RA, Hernández SE, Galindo F, Canales D & Brousset DM (2010) Stress in Wildlife Species: Noninvasive Monitoring of Glucocorticoids. Neuroimmunomodulation 17, 209–212

Ruskell AD, Meiers ST, Jenkins SE & Santymire RM (2015) Effect of Bungee-Carcass Enrichment on Behaviorand Fecal Glucocorticoid Metabolites in Two Species of Zoo-Housed Felids. Zoo Biology 34, 170–177

Saunders SP, Harris T, Traylor-Holzer K & Goodrowe Beck K (2014) Factors influencing breeding success, ovarian cyclicity, and cub survival in zoo-managed tigers (*Panthera tigris*). Animal Reproduction Science 144, 38–47

Sellinger RL & Ha JC (2005) The Effects of Visitor Density and Intensity on the Behavior of Two Captive Jaguars (*Panthera onca*). Journal of Applied Animal Welfare Science 8, 233-244

Skibiel AL, Trevino HS & Naugher K (2007) Comparison of Several Types of Enrichment for Captive Felids. Zoo Biology 26, 371–381

Szokalski MS, Litchfield CA & Foster WK (2013) What Can Zookeepers Tell Us About Interacting With Big Cats in Captivity? Zoo Biology 32, 142–151

8.2.2 Rejected articles

Brown JL (2006) Comparative endocrinology of domestic and nondomestic felids. Theriogenology 66, 25–36

Brown JL (2011) Female reproductive cycles of wild female felids. Animal Reproduction Science 124, 155–162

Claxton AM (2011) The potential of the human–animal relationship as an environmental enrichment for the welfare of zoo-housed animals. Applied Animal Behaviour Science 133, 1– 10

Hill SP & Broom DM (2009) Measuring zoo animal welfare: Theory and Practice. Zoo Biology 28, 531–544

Iossa G, Soulsbury CD & Harris S (2009) Are wild animals suited to a travelling circus life? Animal Welfare 18, 129-140

Jule KR, Leaver LA & Lea SEG (2008) The effects of captive experience on reintroduction survival in carnivores: A review and analysis. Biological Conservation 141, 355-363

Longley L (2011). A review of ageing studies in captive felids. International Zoo Yearbook 45, 91–98

MacDonald E (2015) Quantifying the Impact of Wellington Zoo's Persuasive Communication Campaign on Post-Visit Behavior. Zoo Biology 34, 163–169

Mason GJ (2010) Species differences in responses to captivity: stress, welfare and the comparative method. Trends in Ecology and Evolution 25, 713-721

Mason GJ, Clubb R, Latham N & Vickery S (2007) Why and how should we use environmental enrichment to tackle stereotypic behaviour? Applied Animal Behaviour Science 102, 163-188

Mason GJ, Burn CC, Ahloy Dallaire J, Kroshko J, McDonald Kinkaid H & Jeschke JM (2013) Plastic animals in cages: behavioural flexibility and responses to captivity. Animal Behaviour 85, 1113-1126

Meagher RK (2009) Observer ratings: Validity and value as a tool for animal welfare research. Applied Animal Behaviour Science 119, 1–14

Morgan KN & Tromborg CT (2007) Sources of stress in captivity. Applied Animal Behaviour Science 102, 262-302

Quirke T & O'Riordan RM (2013) Evaluation and Interpretation of the Effects of Environmental Enrichment Utilizing Varying Degrees of Sampling Effort. Zoo Biology 32, 262–268

Stanton LA, Sullivan MS & Fazio JM (2015) A standardized ethogram for the felidae: A tool for behavioral researchers. Applied Animal Behaviour Science 173, 3–16

Szokalski MS, Litchfield CA & Foster WK (2012) Enrichment for captive tigers (*Panthera tigris*): Current knowledge and future directions. Applied Animal Behaviour Science 139, 1– 9

Walker MD, Duggan G, Roulston N, Van Slack A & Mason G (2012) Negative affective states and their effects on morbidity, mortality and longevity. Animal Welfare 21, 497-509

Watson R, Munro C, Edwards KL, Norton V, Brown JL & Walker SL (2013) Development of a versatile enzyme immunoassay for non-invasive assessment of glucocorticoid metabolites in a diversity of taxonomic species. General and Comparative Endocrinology 186, 16–24

Vickery SS & Mason GJ (2005) Stereotypy and perseverative responding in caged bears. Applied Animal Behaviour Science 91, 247–260