Sveriges lantbruksuniversitet
Fakulteten för veterinärmedicin och husdjursvetenskap

On the hunt for improvements –
Possibilities of increasing welfare in captive cheetahs through hunting enrichment.

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Jakten på förbättringar – Möjligheter att öka välfärden hos geparder i fångenskap genom jaktberikning.

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ABSTRACT

The cheetah (*Acinonyx jubatus)* is one of the big feline species kept in zoos worldwide. The wild populations are quite small and therefore the captive population make up an important part of the total population of the world. Although life in the wild is not always easy and a captive environment provides shelter and food it does not come without problems. In captivity cheetahs become chronically ill and also develop stereotypic behaviours. Neither of these are problems in wild populations and both can be linked to stress in captivity. One mean of targeting stereotypic behaviour is to provide environmental enrichments. If it is targeted in the right way then it should reduce stress and may then also have an impact on disease development.

The hunting behaviour of felids can be divided into main sequences of location, capturing, killing and processing of the prey. Since hunting behaviour is a natural behaviour often deprived from the animals in captivity I looked at possibilities of enrichments to stimulate this behaviour. Feasible enrichments could be feeding of carcasses or bones, live bait or a "cheetah run". A cheetah run consists of a moving bait system giving the cheetah an opportunity to pursue lure. Enrichment through live bait or the cheetah run targets the sequences of location, capturing, and killing in the hunting behaviour, while the carcass-feed targets processing of the prey. The enrichments has positive effects on behavioural diversity and behaviour resembling of hunting has been observed in connection to the enrichments. However, the studies reviewed did not show any significant data on the reduction of stereotypic behaviour.

No definite conclusions could be made but findings do suggest a feasibility to improve welfare through stimulation of hunting behaviour. More research is needed and targeting hunting behaviour might not be the most optimal choice, so therefore research need to also focus on evaluating enrichments in connection to other natural behaviours and conditions. Most research up to date focus on studying the effects on one factor e.g. corticoids concentration or stereotypical behaviour. These factors are not reliable on their own and research therefore needs to investigate several factors simultaneously to make more accurate predictions on how welfare is affected. More accurate predictions will lead to clearer guidelines and thereby efforts of improvement can be directed towards areas were most effect will be seen.

SAMMANFATTNING

Geparden *(Acinonyx jubatus)* är ett av de stora kattdjuren som går att beskåda i djurparker världen över. Dess vilda population är ganska liten och därför utgör populationen i fångenskap en betydande del utav världspopulationen. Livet i fångenskap erbjuder både föda och skydd men trots det uppstår en del välfärdsproblem. Geparder i fångenskap insjuknar bland annat i kroniska sjukdomar och uppvisar stereotypa beteenden. Båda problemen kan kopplas till stress i fångenskap och ses inte i de vilda populationerna. Genom miljöberikning kan man arbeta för att minska problemet med stereotypt beteende.

Jaktbeteendet hos kattdjur kan delas in i fyra olika sekvenser: lokalisering, tillfångatagande, dödande och bearbetning av bytet. Eftersom jaktbeteendet är ett naturligt beteende som djuren i djurpark sällan får möjlighet att utföra har jag studerat möjligheter som finns för att stimulera detta genom miljöberikning. Berikningar som kan användas är utfodring med slaktkroppar eller ben, levande byte och ”gepardlopp”. Ett gepardlopp består av ett rörligt byte av något slag som stimulerar geparden till att förfölja det och därmed utföra jaktbeteende. Miljöberikningarna visade sig ha en positiv effekt på beteende repertoaren och jaktbeteenden kunde observeras i anknytning till berikningarna. Däremot så visade ingen av studierna att berikningarna signifikant minskade de stereotypa beteendena.

Det är svårt att dra några säkra slutsatser, men resultaten antyder att man genom jaktberikning möjligtvis kan förbättra djurens välfärd. Mer forskning behövs och att fokusera på berikning av jaktbeteendet kanske inte är optimalt, så därför borde forskningen också fokusera på att utvärdera berikning med koppling till andra naturliga beteenden och förhållanden. Hittills har forskningen främst fokuserat på att studera berikningars effekt på en faktor, så som värden av stresshormon eller stereotypa beteenden. Att analysera dessa faktorer enskilt ger inte pålitliga resultat och forskningen måste därför undersöka flera faktorer samtidigt för att göra säkrare förutsägelser om hur välfärden påverkas. Säkrare resultat gör att tydligare riktlinjer kan upprättas och insatser till förbättring kan riktas mot områden där de har mest effekt.

INTRODUCTION

The cheetah (*Acinonyx jubatus)* is a big feline animal, the world's fastest mammal (Nationalencyklopedin) and listed by the IUCN Endangered Species commission as a vulnerable species (IUCN, 2013). The wild population is estimated to between 7000 and 10 000 individuals (IUCN, 2013) and found mainly in south and east Africa. The captive population was in 2011 noted to a number of 1614 (Marker, 2011) therefore making up about at least 13% of the total population of the world. How well we manage this captive population might therefore have a big impact on future conservation of the cheetah as a living species.

Some problems found in the captive cheetah populations are disease and stereotypic behaviour (Mason et al., 2007; Munson et al., 1999; Munson et al., 2005). This review will characterise these problems and since these problems have been linked to presence of stress (Mason, 1991a, 1991b; Munson et al., 2005), the review will further investigate the possibilities of decreasing stress in the captive environment by environmental enrichment. The main focus will then be on stimulation of hunting behaviour since this is often a behaviour deprived from predators in captivity (Lindburg, 1988).

METHODS

With the use of the databases PubMed, Google Scholar, Science Direct, Web of Science, Wildlife & Ecology Studies Worldwide and Primo, literature was searched regarding captive cheetahs and environmental enrichment in connection with hunting behaviour. Included search words were: *Acinonyx jubatus*, cheetah*, captive, free-ranging, disease, stress, stereotypic behaviour/behavior, stereotypy, environmental enrichment, carcass, feed*, hunt*, cat*, felids, feline and mammal*. Reference list in articles found relevant were also used in the search.

LITERATURE REVIEW

Disease in the captive cheetah

In 1988 Gosselin et al. wrote about a disease causing obstruction of the small veins in the liver (hepatic veno-occlusive disease) in the captive cheetah. A more recent long term study by Munson et al. (2005) concluded that the free-ranging cheetah population of Namibia is much less affected by disease than the captive population of North America and South Africa respectively. The most common diseases found in the captive populations were hepatic veno-occlusive disease, glomerulosclerosis, gastritis and systemic amyloidosis (Munson et al., 2005). Munson et al. (2005) also showed that both wild and captive populations were greatly colonised by *Helicobacter spp.* but only 3% of the wild populations had moderate to severe gastritis while the prevalence in the captive population was 64%. Terio et al. (2005) found that different types of *Helicobacter spp.* are found in captive cheetahs with gastritis. The same types were also found in wild healthy individuals, suggesting that host factors are important in the development of gastritis. Genetic factors like inbreeding of captive populations could have an effect but captive and free-ranging cheetah populations are both genetically impoverished to the same degree (O'brien et al., 1983). With that in mind and taking histological findings into account Munson et al. (1999; 2005) suggests that the differences seen between disease prevalence in captive and wild cheetahs are a result of environmental effects causing stress in the captive cheetah. That captive cheetahs are stressed is supported by the findings of Terio et al. (2004)

which showed that captive cheetahs had significantly higher baselines of corticoid concentrations and also larger adrenal cortices compared to the free-ranging cheetahs.

The severest cases of veno-occlusive disease in the captive South African population were found in animals kept in city zoos and not in the rural breeding facilities. This further supports the cause of disease to be environmental (Munson et al., 1999). The fact that being on display may be stressful was also shown in a study by Wielebnowski et al. (2002), where individuals of captive clouded leopard (*Neofelis nebulosa)* on-exhibit had higher concentration of faecal corticoids than the ones housed off-exhibit.

Stereotypic behaviour

Mason (1991a) defines stereotypical behaviour as repetitive, invariant behaviour patterns without a clear goal or function. It often consists out of a movement performed repetitively and which might be difficult for the animal to stop. These behaviours are only seen in captive animals and not in their wild counterparts, and are therefore considered abnormal. Although it is not certain that this makes the behaviours maladaptive Mason (1991a) states, since they often resemble behaviours seen in the wild (making it harder to distinguish the stereotypic behaviour).

Factors eliciting the stereotypic behaviours are situations of stress, conflict and frustration (Mason, 1991a). This is often seen in situations where stimulus input is low, physical movement is restrained and frustration or fear is inescapable (Mason, 1991b). Mason (1991a) then states that motivation leading up to frustration is then often redirected to performing the stereotypic behaviour. She (1991b) further argues that in contrast, factors that give the animal opportunity to perform motivated behaviour will lead to a decrease in stereotypic behaviour with hope of eradicating the stereotypy. She also notes that stereotypy can develop from anticipation. The example of anticipation is illustrated by the behaviour typically seen in carnivores performing pre-feeding excitement behaviour. Once stereotypy is established it commonly appears when stimuli is lacking and arousal is low (Mason, 1991b).

Stereotypical behaviour is often seen in animals that are or have been experiencing sub-optimal housing arrangements and therefore they have been used as an indicator of poor welfare (Mason, 1991a). In fact approximately 68% of factors increasing or causing stereotypical behaviour could be connected to a decrease in welfare according to Mason and Latham (2004). Although Mason (1991b) points out that the degree of stereotypic behaviour performed does not have to correspond to the degree of suffering. She then notes that the level of stereotypic behaviour displayed in one individual might thereby not reflect better or worse welfare compared to other individuals. In fact Mason and Latham (2004) saw that, when comparing animals within a housing system, the animals displaying stereotypic behaviour often fared better than the ones that did not.

Contradicting the theory of stereotypy not having a goal is the theory that stereotypy is rewarding, as animals will continue performing the behaviour even when resulting in self-damage or a very high energy cost (Mason, 1991a). Mason further states that such persistence in behaviour might also be explained by the behaviour being constantly stimulated or by lack of motivation/possibilities to perform other behaviours. The coping theory suggests that the

performance of the stereotypy somehow keeps the animal in physiological and/or psychological balance (Mason, 1991a). Even though this might be true for some stereotypies this does not apply for all, Mason points out. This is because, she explains, stereotypic behaviours differ from each other in both intrinsic, e.g. motivation, and extrinsic attributes, e.g. environmental factors.

Mason (1991a) shows that several findings point to the fact that performing stereotypic behaviour has a calming (lowered arousal) effect and has also been associated with a fall in corticosteroid levels. For example individuals that are being hindered to perform their stereotypic behaviours show an elevated level of corticoids (Mason, 1991a). Although this correlation is not always true, in a study by Wielebnowski et al. (2002) the individuals performing stereotypic (self-injuring) behaviour had higher levels of corticoid concentrations than those who did not perform such behaviours. Mason (1991a) further points out that some data however reveals that hormone levels influence the behaviour rather than behaviour influencing the hormones.

Mason (1991b) argues the characteristics of stereotypic behaviour doesn't make it a reliable indicator of well-being but should not be ignored as a potential one. In support of this Mason et al. (2007) argues that since stereotypic behaviour has been linked to poor welfare it should always be taken seriously. The prevalence of stereotypy has been reported at up to 82% percent in captive carnivores (Mason & Latham, 2004). More specifically Lyons et al. (1997) found that 79% of the captive felids were performing the stereotypic behaviour of pacing. They defined pacing as movement back and forward, often on a fixed route within the enclosure. In a cross-institutional study the main stereotypic behaviour performed by the cheetah was shown to be pacing and the behaviour was noted in 85 out of 88 enclosures studied (Quirke et al., 2012).

Stimulating hunting behaviour through environmental enrichment.

As seen above keeping predators like cheetahs in captivity poses a problem. When using the hunting behaviour as a model for enrichment in captivity, Lindburg (1988) suggested to aim efforts towards the areas of activity and food packaging. This is further supported by Carlstead (1998) suggesting that stereotypes in carnivores are much explained by the frequency and method of feeding. Shepherdson (1998) points out that when working towards an optimal environment in captivity one should focus on stimulation of natural behaviour and thereby providing the animals a chance to exhibit the behaviours they would in the wild.

Hunting behaviour

When studying the hunting behaviour of large felids in the wild Lindburg (1988) found that their quest for food as predators consist out of a series of energy demanding activities. He then suggested that these behaviours would be divided into four main activities: location, capturing, killing and processing of the prey.

Lindburg (1988) then further defined location of prey to consist out of both travelling and detection of the prey. Upon detection, the next step of the hunt was capturing of the prey. This consisted out of different behaviours like stalking, ambush and sprinting. Lindburg (1988) noted that stalking was the most common among the cheetahs and that they would begin their

capture sprint up to 250 meters or further away from the prey. During the sprint a cheetah might reach speeds up to 29m/s or 103 km/h. (Sharp, 1997).

At the end of the chase, when the killing takes place the light cheetah depends on the prey loosing balance after trying to trip it and once prey is taken down cheetahs will kill it by biting the throat, inducing strangulation (Lindburg, 1988). Lindburg further noted that after the kill, cheetahs would move its prey and then rest for approximately half an hour before starting to feed. Once prey was caught cheetahs ran the risk of losing their prey to other carnivores so they stayed with the carcass for one single feeding (Lindburg, 1988).

When studying wild cheetahs Cooper et al. (2007) found that decisions to hunt are mainly based on abundance of main prey, reproductive status (presence of cubs) and presence of competitors or predators (such as lions). They did not find significant proof that hunger affects the decision. Presence of cubs and high presence of prey affected the decision positively while presence of predators/competitors in form of lions had a negative effect (Cooper et al., 2007). The effect of competitors/predators has also been shown by Durant (1998) which noted that wild cheetahs, when in close proximity to lions would chose avoidance by moving away rather than hunting.

Environmental enrichment

Manipulation of food.

Food provisioning in captivity often consists of commercially prepared formulations with little or no opportunity for processing the food before ingesting it (Lindburg, 1998). Such feeding regime Lindburg argues, deprives predators of a natural behaviour associated with the hunt, processing of the prey. Already in 1988 Lindburg noted that supplementing carcasses to captive felids increased appetite and playing behaviours.

When Bashaw et al. (2003) looked at the effect of feeding bones twice per week to African lions (*Panthera leo)* and Sumatran tigers (*Panthera tigris sumatrae)* no significant differences could be seen but data still revealed a tendency towards increased non-stereotypic activity and a decreased time pacing. Skibiel et al. (2007) also studied the effects of supplementing bones to felids and found that active behaviours increased but the effect was not sustained seven days post enrichment. They also saw a decrease in stereotypic behaviour but it was not statistically significant.

A study (McPhee, 2002) looking at different effects seen when feeding on- and off-exhibit of whole calf-carcasses (eviscerated upon veterinarian's request) found an overall increase of feeding behaviour off-exhibit. An overall increase in natural behaviours was also seen. On exhibit there were no significant effects shown by the enrichment, neither natural behaviours increased nor stereotypical behaviours decreased (McPhee, 2002).

Mellen et al. (1998) have also noted that many felids, upon receiving whole or parts of carcasses display a behavioural sequence similar to the stalk-rush-kill sequence seen in the wild.

Live bait

Presenting cheetahs or other felids with live prey can be debated from an ethical standpoint. Depending on the law of the country this might also be possible or not. For example Swedish

law states that animals in zoos should be kept in a way that protects them from predator attacks (Jordbruksverket, 2009) so placing a live bait in the enclosure of a predator wouldn't be possible. Independent of law or ethical dilemma felids like Sumatran tigers (*Panthera tigris sumatrae)* and Fishing cat (*Prionailurus viverrinus)* have been shown to change behaviour patterns when being presented with live fish (Bashaw et al., 2003; Shepherdson et al., 1993)

In the study conducted on Sumatran tigers by Bashaw et al. (2003) the animals were supplied with live fish twice a week during four weeks. There were no statistically significant changes, only two animals were observed, but raw data revealed an almost 50% reduction of pacing during two days following the enrichment. On the mornings before the fish sessions started some appetite behaviours like biting, swiping, crouching and pouncing could be seen. These behaviours were not included in the data collection and only seen in this specific situation (Bashaw et al., 2003). Similar results were obtained when feeding live fish to Fishing cat, which showed a decrease in time spent sleeping and an increase in activity and behavioural diversity extending beyond the day of enrichment. (Shepherdson et al., 1993)

Cheetah run

"Cheetah run" is an enrichment which is used more often in zoological institutions where cheetahs are kept (Ziegler-Meeks, 2009) and designs vary a lot between different institutions. Even so they all consist of devices with a moving bait system that aim to give the cheetah an opportunity to pursue lure and trough that promoting activity and hunting behaviours (Quirke et al., 2013).

The effects on the behaviour of captive cheetahs by the use of moving bait were studied by Williams et al. (1996). In their study a device consisting of pulley carriages and a rope was used. The device was activated by dropping the bait over the fence on one side of the enclosure which then proceeded to cross the enclosure. If the cheetahs had not caught the prey when it reached the other side it was lifted up, out of their reach. After collecting baseline information, the cheetahs were trained for two weeks to take food from the device. Then followed the enrichment period during which the cheetahs were fed one whole rabbit as bait from the device for ten following days. Post-enrichment behaviour was also observed. Williams et al. (1996) noted that during the enrichment period, when preparations of the device started, the cheetahs would prepare for the chase by crouching close by where the bait would appear. When activated the cheetahs waited until the bait passed them and then began to pursue it. They then caught the prey by striking it and once caught carried it away to consume it directly. Significant effects on behaviour was found and showed an increase in vigilance behaviour when using the device compared to baseline. A decrease in affiliation between the two cheetahs kept together comparing enrichment and post-enrichment was also noted. Feeding time was also decreased, significantly so when fed through the device. Furthermore the cheetahs displayed a significant change of behavioural diversity with an increase with device and post-enrichment compared to the baseline (Williams et al., 1996).

Another study, taking a comparative approach to highlight the difference between separate zoological institutions and their designs of the cheetah runs was done by Quirke et al. (2013). The cheetahs studied came from Fota Wildlife Park, Ireland; Ann van Dyk Cheetah Center

(AvD), South Africa and Cheetah Conservation Fund (CCF), Namibia. The cheetah runs differed in design and length. At AvD and CCF the hunting target consisted out of a rag or white plastic that was attached to a car starter motor. This design is similar to techniques used in coursing grey hounds. At Fota the target consisted out of a whole rabbit or chicken hanging from a wire off the ground. In all three systems both speed and directions of the lure could be controlled. For some of the cheetahs the device was new and some had already been trained. The training consisted out of conditioning through positive reinforcement to return to the operator to retrieve reward after pursuing the lure. A reward was only given if the track was completed (Quirke et al., 2013).

To evaluate the different designs Quirke et al. (2013) measured speed and gait during the runs. Several recordings of the runs were made and in the analysis the highest speed for each individual cheetah was used. The highest speed attained during the study was 100.1 km/h by a female in AvD. In average females attained higher speeds than males and trained cheetahs attained higher speeds than untrained ones. Both these findings were statistically significant. When comparing results between the zoological institutions there were some differences noted but the only statistically significant difference was found between AvD and CCF, with cheetahs at the AvD attaining higher speeds then in the CFF (Quirke et al., 2013).

The difference between the zoological institutions seen in the study by Quirke et al. (2013) might be explained by the AvD cheetahs being trained while the ones at CFF had not been trained and did not receive a reward as a result of pursuing the lure. These factors as well as frequency of runs per week and group constellations during the run may also have influenced the result since they differed between the institutions. Another factor influencing the difference between the AvD and CFF was the design of the track. Both consisted out of similar areas of cover but differed in size. The CFF had the largest run and a squared shape while the one at AvD was shorter and shaped like a U, with turns being implemented in one of the straight parts of the track. The large track at the CCF resulted in that the cheetahs frequently observed lure from the other side of the track and would walk in the direction of the lure and very rarely engaged in longer chases. In the AvD the design of the track ensured that the animal always was in close proximity of the lure possibly increasing the motivation (Quirke et al., 2013).

DISCUSSION

Some of the welfare problems with keeping cheetahs in captivity are connected to stereotypic behaviour and disease. These are problems that seem to be triggered by the captive environment itself. Therefore it is important that we regard them in the management of these animals and try to tackle them the best we can. Suggestions have been made to tackle these problems through environmental enrichment. In this review I have specifically looked at stimulation of the hunting behaviour. But what do these findings tell us?

Why we should care

Mason and Latham (2004) point out that although stereotypic behaviour is not always a good indicator of poor welfare it should never be disregarded as it may indicate suffering. If the stress of captivity is causing the display of stereotypic behaviour then I believe that the behaviour should definitely be regarded as an indicator of both poor welfare and health. Health should be

included since the same stress that is causing the abnormal behavioural patterns might also be the direct cause of or in some extent contribute to disease development. Disease in itself can cause suffering but will also affect the longevity of the animal. I believe this is of economic importance for the zoos since, apart from funding costly treatments, it will need to acquire more animals in the same amount of time compared to if the animal would have lived longer. Furthermore an animal being unwell could mean that it needs to be taken off-exhibit which might then cause stress in individuals remaining in the enclosure and so possibly increasing the risk of making them more prone to develop disease. It is also possible that animals missing on-exhibit may affect the public's perception of the zoo in a negative manner, simply because the zoo doesn't show the animals they promise. Animals on-exhibit displaying stereotypic behaviour might also affect the public's perception since visitors, as Carlstead (1998) states, always perceive these animals as being stressed, bored or anxious. Carlstead furthermore argues that the stereotypic behaviour is also a distraction from the educational value of the animals since they are no longer displaying natural behaviours. If zoos can't pose as educators and evoke fascination in the animals then I believe there is a risk that, in a long term perspective, this might affect interests and concerns regarding the conservation of the wild species.

Although the animals displaying the stereotypic behaviour might attract the most attention by visitors it is important to remember that these are not always the animals suffering the worst. The stereotypic behaviour might be a way of coping with their stress and in fact the most passive animals might be the worst off. Whether a stereotypic behaviour is a means of coping or not seems to vary between situations and individuals. Nonetheless the display of stereotypic behaviour tells us that the housing of that individual/group is in some way inducing stress in the animal/-s.

Furthermore, development of stereotypic behaviour and disease can have an effect on the direct conservation of the species. If the aim is to produce an offspring in captivity to then re-introduce into the wild, the development of unnatural behaviours rather than natural behaviour seen in the wild might affect that individual's change of survival if released. If the animal then also is a carrier of chronic disease it will not be given a good chance at survival in the wild and will definitely have a disadvantage to its wild born conspecifics. The case of stereotypic behaviour is further complicated by the fact that some stereotypic behaviour might be caused by dysfunction of the central nervous system, as suggested by Mason et al. (2007). To introduce such a dysfunctional individual to a wild population would then, in my opinion, be wrong as it would be given a chance to spread its DNA and possibly contribute to a weakened fitness trough out that population.

To conclude, since stress seems to be a factor of importance in development of both stereotypic behaviour and disease, I suggest that actions directed towards eradicating stressors in the environment should be a priority. If stereotypic behaviour is caused by stress from being unable to perform motivated behaviours, as suggested by Mason (1991a, b), then it seems plausible that some stress could be reduced by stimulating natural behaviours such as the hunting behaviour. It is important however to note that there are many other factors that might impact stress levels in the captive environment. For example a study by Wielebnowski et al. (2002) found effects in stress hormone levels depending on presence of potential predators and keeper-

animal interactions. Quirke et al. (2012) also showed how enclosure size and feeding-regime can affect the prevalence of stereotypic behaviour and thereby implying reduced or increased levels of stress.

Effects of stimulation of hunting behaviour

The literature shows that supplying carcasses or bones as an environmental enrichment have positive effects such as increased active behaviours e.g. appetite, hunting, playing and social behaviours. A decrease in stereotypic pacing was seen in one study (Skibiel et al., 2007) but the result was not statistically significant. Very few findings in the literature were proven to be statistically significant and some are mere observations, therefore it's important to be careful during interpretation of these findings. Although one should bear in mind that small study groups, which are often the case, might partially explain why so few results could be proven significant. It is therefore my opinion that these findings should not be totally discarded and further research needs to establish the effect that this specific environmental enrichments has on stereotypic behaviour. One conclusion that can be made is, that there are no indications of a decrease in welfare when feeding carcasses or bones to the animals. This is also neither expensive nor particularly difficult to provide. Furthermore a positive effect on oral health has been suggested by Bond and Lindburg (1990) but the findings of Munson et al. (1999; 2005) show that it's unlikely to have a long term effect on the development of chronic disease in the captive populations. Their studies showed that cheetahs from the captive South African population being fed carcass or unprocessed meat, much like the diet of their wild conspecifics, have similar disease prevalence as the captive North American population fed with processed meat.

No studies to my findings reports of effects on live prey to captive cheetahs. Instead the studies found concerned other feline species (Sumatran tigers and Fishing cat) which were supplemented with live fish. Positive effects on behaviour were seen in both studies and in the study of Fishing cat (Shepherdson et al., 1993) the increase in behavioural diversity extended past the day of enrichment. For these felines, fish is part of the natural diet and therefore the studies can serve as an indicator of potential effects of introducing live prey as an environmental enrichment to other captive felines. I do not argue that live prey should be used for the purpose of environmental enrichment, as I believe that it would not be appropriate taking the prey animals' welfare into account. Instead I suggest that these findings should serve as an indication of how "live like" prey presented to the cheetahs could have a positive effect on welfare.

An example of such "live like" prey enrichment is the cheetah run. Williams et al. (1996) studied its effect on behaviour and found that it increased the behavioural diversity and vigilance behaviour. The effects on behavioural diversity even extended into the post-enrichment period. Although this is only one study, it indicates that the cheetah run can be an effective tool to elicit a wider range of behaviours. The sequence similar to stalk-rush-kill behaviour noted by Williams et al. (1996) suggests a stimulation of hunting behaviour. Quirke et al. (2013) didn't study effects on behaviour but looked at the speed attained in different designs of the cheetah run. Since the aim of environmental enrichment is to stimulate natural behaviours one can assume that attaining speeds in captivity similar to the ones in the wild can be a good measurement of the designs efficacy. Although the variation in speed attained and its

effect on behaviour, health and welfare needs to be further investigated, this study still gives rise to questions of how one should design and manage an optimal cheetah run. The results e.g. indicates that training with the bait-device and receiving a reward from keepers, when completing a chase, gives rise to higher speeds. When deciding whether to reward and train the animals or not, one should bear in mind what the purpose of keeping the animals are. I believe that the human interaction, which positive reinforcement training would imply, is not a natural behaviour and will not be productive if the animals are to be re-introduced into the wild. So maintaining naturalistic enrichments can be important, this is supported by Mason et al. (2007) suggesting that naturalistic enrichments might enhance the animals' conservation value. In the same time they also point out that the effectiveness of environmental enrichment might increase if non-stereotypic behaviour is positively reinforced. So on the other hand, if the animals are to stay in captivity, training might be of benefit. It might then also lead to a desensitisation of human interactions and thereby potentially decreasing stress induced in animals on-exhibit. Research comparing how well trained and untrained animals respectively deal with the stress of visitors on-exhibit would definitely be useful in this context.

I'd like to point out that it's hard to conclude anything from the studies reviewed since so few animals have been included and probably no selection has been made. Animals were probably studied based on the possibilities of conducting research in the zoological institutions rather than based on inherent features of the animals themselves. Furthermore it should be noted that when interpreting results of environmental enrichments effects on behaviour some questions should be posed. For one thing, are the effects we are observing effects of the specific enrichment or purely an effect of novelty? To investigate this further, research need to evaluate effects in a long term perspective. Secondly, are the right behaviours targeted in the right way? Mason et al. (2007) points out that if the environmental enrichment does not target the underlying frustration it might still reduce stereotypic behaviour by reducing factors contributing to stress or by distracting the animals from performing stereotypic behaviour (by offering stimulus for other preferred behaviour). How to interpret behavioural studies are further complicated by the fact that some stereotypic behaviours might be resistant to change once established, as stated by Mason et al. (2007). Although the lack of effect, they point out, might also originate from the enrichment not being optimal. Adding these factors together might explain why, to my findings, no study has shown stereotypic behaviour to be totally eradicated in zoo animals.

It is possible that the enrichments reviewed in this thesis are not optimal. In fact in a meta-analysis of carnivore stereotypes Clubb and Mason (2007) found no correlation between foraging variables and stereotypic pacing. More in detail this means e.g. that species of carnivores with a higher frequency of hunts and kills per day then others does not perform stereotypic behaviour to a greater extent than the ones with a lower frequency. Instead stereotypic pacing correlated with a greater distances of daily travels, meaning that carnivore species travelling far and wide in the wild have a higher risk of developing stereotypic behaviour in captivity. Clubb and Mason (2007) therefore suggest that increased size of enclosures could target this problem. Due to its practical limitations they argue that instead analyses should be made investigating what this daily travel distance means for the animal so that different aspects of the behaviour can be stimulated separately. If one of these aspects is

activity, then providing cheetahs with a stimulus to hunt should increase the level of activity and therefore potentially targeting the underlying problem.

Final remarks

To conclude it seems feasible to improve the welfare of captive cheetah's trough environmental enrichment aiming to stimulate hunting behaviour but more research is needed. Most research to date focuses on studying the effect of one factor e.g. corticoids concentration or stereotypical behaviour. As we have seen studies show that these factors can correlate both with an increase and decrease in welfare. Therefore it is hard to evaluate the welfare based upon only one factor. I hereby suggest that research should aim to look at several factors simultaneously and that to evaluate effects on health, measurements of morbidity should be included. With more data we can work on optimising the enrichment provided to these animals and focus on eliminating as many stressors as possible.

I lastly argue, with welfare in mind, that facilities keeping cheetahs should do everything in their power to improve the captive situation of these animals since the problems reviewed are very real. This I argue not only for the sake of the individual animal but also for the sake of education, appearances of zoos and conservation efforts.

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