



Do prey-animals in zoos need predators?

Behöver bytesdjur i djurparker predatorer?

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I denna serie publiceras olika typer av studentarbeten, bl.a. examensarbeten, vanligtvis omfattande 7,5-30 hp. Studentarbeten ingår som en obligatorisk del i olika program och syftar till att under handledning ge den studerande träning i att självständigt och på ett vetenskapligt sätt lösa en uppgift. Arbetenas innehåll, resultat och slutsatser bör således bedömas mot denna bakgrund.

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1. Sammanfattning

Idag är ett av målen med djurparker att bevara hotade djurarter och vissa djur kan även planeras att bli återintroducerade. Men beteende kan förändras genom generationer hos djur i fångenskap på grund av att miljöerna är annorlunda än i det vilda. Därför måste djur förberedas innan återintroduktion och predator träning ökar chansen för djuren att överleva i det vilda. När djur tränas för att undvika rovdjur behöver man ofta använda sig av skrämmande stimuli. Men det har även visats sig att erfarna demonstratörer kan förbättra oerfarna yngre djurs inläring om predatorer. Dessa djur har även visat sig vara mer framgångsrika i återintroduktioner. På djurparker används berikningar för att erbjuda djurparksdjur naturliga miljöer och möjligheter att utföra naturligt beteende. Men för att behålla djurets naturliga beteenden som skulle kunna vara till fördel inför framtida återintroduktioner, borde man även utforma specifika program för anti-predator beteenden. Program för att behålla sådana naturliga beteenden kan dock krocka med etiska principer och djurens välfärd, vilket gör att planering och utvärdering av skrämselferikningar är viktigt. För att använda sig av skrämselferikningar kan ett sätt vara att använda visuella modeller på grund av att bytesdjur verkar ha ett inbyggt system för att visuellt känna igen rovdjur.

2. Summary

Today is one of the goals with zoos to conserve endangered species and some animals may also become reintroduced. But behaviours can change in generations of captive animals because of environments that differ from the wild. Animals must then be prepared before being reintroduced and predator training enhances the animal's chance to survive in the wild. When training animals to avoid predators it is often necessary to use frightening stimuli. However, it has been shown that experienced demonstrators improve unexperienced juveniles' learning about predators. These juveniles also seem to be more successful in reintroductions. In zoos enrichments are used to provide animals with natural environments and possibilities to perform natural behaviours. But in order to keep natural behaviours that could be advantageous in future reintroductions, specific anti-predator behaviour programs should be developed. But programs for retaining such natural behaviours can be in conflict with ethical principles and animal welfare. This makes it more important to carefully plan and evaluate anti-predator behavioural programs. Using visual models could be one approach when designing enrichments, this because prey-animals seem to have an innate system for recognizing predators visually.

3. Introduction

3.1. Background

One of the most important reasons for keeping animals in zoos is conservation (Kleiman et al., 2010). Over the past decade the cooperation for captive-breeding programs has increased and zoos are cooperating internationally for populations according to genetic principles (Wielebnowski, 1998; Kleiman et al., 2010). Zoos are also becoming more involved in reintroduction programs for animals that have been born in captivity and the ultimate goal is to re-establish populations in the wild.

Individuals interact with their environment through behaviour and there are many behavioural factors that affect survival (Blumstein, 2000). According to Maran (2003) captive animals do not have the experience and skills that are required to survive in the wild. This may lead to a high mortality rate during the first period of release and by breeding period there will be too few animals left for founding a viable population. Animals that are allowed to perform and maintain species-appropriate behaviours seem more successful when reintroduced into their natural habitat (Mellen & McPhee, 2001). Therefore it is common that behavioural skills of endangered species in captivity are manipulated, for example by feeding animals in a natural way, giving access to necessary habitat requirements and maintaining animals in natural social groups (Kleiman et al., 2010). But one thing that is seldom attempted is for captive prey animals to recognize predators.

The role of experience in the development of anti-predator behaviour is of importance and should be further investigated (Shier & Owings, 2007). Captive animals live in an environment that might not provide experiences necessary for surviving in the wild. For animals to better survive and reproduce in their native habitat, behaviours evolve over generations in complex environments (Hosey et al., 2009; Kleiman et al., 2010). The behaviour of captive animals can be affected by differences between captive and native environments and can diverge from that of their wild counterparts (Kleiman et al., 2010).

When keeping wild animals in captivity, animal welfare is a key management issue (Kleiman et al., 2010). An important aspect of overall zoo management is therefore to try to minimize the stress that animals might experience and natural behaviours are important when measuring welfare. A lot of focus is attended to behavioural needs of animals for their well-being, but it should perhaps be more intention to preserving appropriate behaviours (Rabin, 2003). Enrichments have the purpose to reduce unnatural behaviours and provide possibilities for the animals to perform natural behaviours and activity patterns (Mellen & McPhee, 2001). Enrichments have become very important in working with zoo-animals and the most studied animals in captivity are felids and ursids which often display stereotypic behaviours (Swaisgood & Sheperdson, 2005). Performed stereotypic behaviours include abnormal behaviours and imply that an animal is experiencing a welfare challenge (Kleiman et al., 2010). Small felids in captivity often pace repetitively and/or spend a lot of time inactive (Sheperdson et al., 1993). But when presenting the felids to live-fish, Sheperdson et al. (1993) noticed that they were more active and increased their

behavioural diversity, i.e. expressing natural hunting behaviours. How food is presented seems to be important and natural behaviours can be guidelines to enrichments (Mellen & McPhee, 2001). Greater attention is still needed for keeping behaviours in their appropriate contexts and it is important to develop management programs for preserving behaviours of captive-animals (Rabin, 2003).

Behaviours are responses made to stimuli and stimuli can be perceived from the physical environment or other animals (Hosey et al., 2009). But behaviours may also be performed when certain stimuli are absent and the animal is strongly motivated to perform specific behaviours (Hosey et al., 2009; Kleiman et al., 2010). According to Young (2003) has the animal no internal motivation to express the anti-predatory behaviour, if it is not exposed to a predator. Trough evolution prey animals have got morphological, behavioural and life history strategies to avoid being killed by predators and to guarantee leaving off-springs (Blumstein, 2002). Even though prey-animals may not have an internal motivation to express anti-predatory behaviours, it could perhaps be of other importance for the animal. Therefore I want to investigate if animals in captivity need to be enriched with predators. If so, this would also be of value for reintroduction programs.

3.2. Purpose

The purpose of this study is to review scientific research about anti-predator behaviour and investigate if there is a need for enriching zoo-animals with predators and how enrichments could be developed.

- Is the prey-predator interaction important for the prey and if so, is it important for a prey animal in captivity?
- Do anti-predatory behaviours change in captive animals in generations?
- Is anti-predator behaviour important in reintroductions?
- How can captive animals be trained in recognizing predators and performing appropriate anti-predatory behaviour?
- Would it be possible to have predator-enrichments for animals in captivity without affecting welfare negatively?

4. Material and Methods

I have by reviewing scientific literature and books tried to find answers to my questions. I have had a wide perspective and have not been concentrating on any specific species. The search engines on internet I have used are Web of Knowledge, Exlibris Metalib and Google Scholar. Searchwords that I have used are *anti-predator behaviour*, *anti-predator response*, *stress response*, *isolation from predator*, *prey animals*, *anti-predator training*, *welfare*.

5. Results

5.1 Anti-predator behaviour

Recognition of predators is an important part in anti-predator defence mechanisms (Caro, 2005). The prey must recognize danger first in order to use defence behaviour, it must thereby be able to separate a danger situation from a safe and then make the right decision. But a situation where a specific animal become stressed might not apply to an animal of another species or population because of environmental and biological differences (Stankowich, 2008). When the prey animal recognizes danger it notices a threat and this can be measured in simple reflexes like changes in cardiac response (Caro, 2005). A stimuli meaning threat can be classified at different levels as recognizing an individual predator, a hungry individual, a certain species of predator, a certain class of predators like terrestrial or aerial, or a threatening situation that does not always have to involve a predator.

Avoiding predators includes using behavioural, morphological, physiological and life history characters and prey animals recognize danger with cues including sight, sound and odour of predators (Caro, 2005). But adaptations to reduce predation risk are most often very costly, for example when energy must be allocated to producing morphological defences instead of offspring, or vigilance instead of foraging (Blumstein, 2002). Benefits of energy intake and costs of being captured must also be balanced by the animal and when it will become too costly for an animal to stay it makes the decision to flee (Lima, 1998; Stankowich, 2008). A starved animal will probably accept a greater risk of predation while feeding, because it must feed at a high energy intake to survive (Lima, 2008).

Maintaining a balance and steady state is often called homeostasis and something that affects this state is called a “stressor” (Morgan & Tromborg, 2007). Stressors result in several of physiological events that will prepare the body for homeostatic challenge and a coping response, this is called the fight or flight response (Morgan & Tromborg, 2007; Kleiman et al., 2010). When responding to stressors the autonomic activity increases and shifts in the metabolic profile of an animal as it adjusts to some perceived threat from the surroundings (Morgan & Tromborg, 2007). Behavioural responses of orientation, alarm and increased vigilance are associated with short-term stressors and physiological responses are tachycardia, increased respiration rate and increased glucose metabolism. There is also an increase in glucocorticoids which facilitates the mobilization of energy reserves instead of conservation.

For some species there might be a greater risk for being attacked and captured when fleeing, therefore they use the strategy to stay put and fight (Lingle & Pellis, 2002). This applies for mule deers (*Odocoileus hemionus*) which seek out rugged terrain or elevated points and stay close together in groups. Ungulates that are in the same size as mule deers use aggression only when defending off-spring. Somehow mule deers, even though they are relatively small, are able to use a strategy of confrontating coyotes. But a lonely mule deer is at greater risk to being attacked and flight can be a good temporary tactic for improving its position, therefore individuals are expected to locate groups to join. For animals that live in groups, the risk for the individual prey to be selected and captured decreases when group size increases (Blumstein & Daniels, 2005). Individuals should also spend less time

to vigilance and more to foraging since there are more group members that can detect predators. But more members in the group also increase the time allocated to foraging due to competition (Blumstein, 2000).

5.1.1. Social learning

According to Caro (2005) certain species of prey animals might be able to respond to predators correctly on their first encounter. If predation pressure is high after being born or hatched or there are limitations in learning about predators, it is likely that innate anti-predator behaviour is manifested. But in species that have long-lasting bonds between parents and juveniles, learning about predator avoidance or recognition from parents may occur (Griffin, et al., 2000).

Beani & Dessí-Fulgheri (1998) studied defensive behaviour of two different groups of Grey partridges (*Perdix perdix*), one group was parent-reared and the other one was intensively-reared. For partridges effective behaviours towards aerial predators in open fields are freezing, crouching and sustained vigilance (Beani & Dessí-Fulgheri, 1998). The results in the study were that parent-reared partridges showed a stronger response and performed more often anti-predator behaviours than intensively reared birds. This indicates that rearing methods influence anti-predator behaviour and fine tuning of responses. Effectiveness is then increased during association with parents (Griffin et al., 2000).

Social effects were also demonstrated by Shier & Owings (2007) who studied effects of social learning in the black tailed prairie dog (*Cynomys ludovicianus*). Captive-reared juveniles were trained in two groups, one with experienced adult demonstrators and the other without demonstrators, with exposure to three predators. After trainings, juveniles trained with an experienced adult were more wary towards predators than the other group. They alarm-called more frequently, were more vigilant and less active and spent more time in shelter when being exposed to predators. The juveniles seemed to attend to the behaviour of the demonstrator and changed their responses to stimuli.

5.2. Isolation from predators

Because of anti-predator adaptations being costly it is expected when predators are removed that morphological and anti-predator defences will be lost and life-history strategies shifting to parental-investing (Blumstein, 2002).

McPhee (2003) studied wild caught oldfield mice (*Peromyscus polionotus subgriseus*) and generations of wild caught mice that were held in captivity. The results showed that an individual from a population which had been in captivity for the longest was the least likely to take cover after a predator had been presented. There was also an increase in variance in predator-response behaviours with generations. For an animal in captivity there are no trade-offs in allocating energy and which response a mouse ever did in the study would not affect survival or success in reproduction (McPhee, 2003). This is called relaxed selection when certain behaviours that would have been selected against in the wild are possible to express in captivity (Kleiman et al., 2010). Animals in the wild must respond fast to recognize a predator and flee, but captive animals can respond immediately or never to fearful stimuli which increases the variance in response time.

Isolation does not only exist in captivity but can also exist naturally on islands. Blumstein & Daniel (2001) studied antipredator behaviour of tammar wallabies (*Macropus eugenii*) and western gray kangaroos (*Macropus fuliginosus*) in Australia in order to understand how behaviours can change by losing some or all predators. In one of the studied area large diurnal raptors lived that could prey on small mammals, but tammar wallabies and the bigger western gray kangaroos are active at nights and there were no risk of nocturnal aerial predators. But in the other studied area both species had consistently been exposed to predators through history. The results of the study revealed that both species were more wary in the riskier site. However, kangaroos only exhibited group-size effects in the riskier area meanwhile wallabies did at both sites. This indicates that presence of a predator may affect the selection and an integrated anti-predator system will be maintained (Blumstein & Daniel, 2001).

Even when there is only one predator species in the environment, anti-predator behaviour which is effective for other predators may persist (Blumstein et al., 2004). For example, in one study (Blumstein et al., 2000) tammar wallabies with aerial predators in their environment recognized novel mammalian predators, while tammar wallabies without predators did not. Interestingly, the duration prey animals have been isolated from predators might not affect anti-predator behaviour. Tammar wallabies, that have been isolated for 130 years, did not recognize predators while tammar wallabies that have been isolated from mammalian, but not avian predators, for 9500 years did recognize novel predators (Blumstein et al., 2004).

5.2.1. Hardwired and flexible behaviours

In a study by Blumstein et al. (2000) captive tammar wallabies were exposed to certain artificial predators that did not exist in their natural environment. The tammar wallabies showed anti-predator behaviour by increased vigilance, decreased foraging and thumping their foot which suggests that visual predator recognition abilities might be hardwired (Blumstein, 2002). In the same study by Blumstein et al. (2000) sounds were also played to characterize responses to acoustic cues from predators and conspecific alarm signals. The sounds of predators did not give a reaction, however the sounds of conspecific anti-predator signal lead to less foraging and increased vigilance by the tammar wallabies. The reason for recognition of visual cues persists in generations, even when the selection is relaxed, might be because of common shared features among predators, for example similar raptor silhouettes (Blumstein et al., 2000, Blumstein, 2006). Another example is carnivores that have binocular vision and positioned eyes and the presence of eyes or eyelike structures often triggers an anti-predator response by the prey-animal (Blumstein et al., 2000; Caro, 2005). Behaviours should not evolve independently and that is why prey-animals seem to have an integrated predator recognition system (Blumstein, 2006).

Behaviours that rely on experience change rapidly when animals are isolated from predators, on the other hand, behaviours that are more hardwired can still be kept (Blumstein, 2002). Fleeing is a behaviour that is very flexible, and it has been seen that isolated animals on islands may be less wary than animals on mainland (Blumstein & Daniel, 2001). Fleeing behaviour is probably dependant on experience with predators, as are recognizing olfactory and acoustic cues for proper performance (Blumstein & Daniel, 2001; Blumstein, 2002).

Blumstein (2002) suggests that behaviours that rely on experience have immediate costs and recognition-errors are costly. An animal that flees from a non-existing predator has to use unnecessary energy and loses an opportunity for example in foraging. Therefore, responding to olfactory cues or sounds is risky and when the cues do not involve a predator it is waste of energy and could reduce fitness. However, Buchanan-Smith et al. (1993) studied responses of 56 captive cotton-top tamarines monkeys (*Saguinus Oedipus*) to faecal scent of predators and non-predators. The monkeys were also divided into two groups, one with wild-caught parents and one with captive-born parents. Behaviours expressing anxiety was considered as “approach dowl (with faeces) and withdraw” and “sniff and run”. The results were that monkeys showed high anxiety responses to predator scent and low anxiety and more curiosity responses to non-predator scent. There was no significant difference between groups either and these results indicate that being able to discriminate predator scents from other scents is innate.

5.3. Reintroduction

Some animals are planned to be reintroduced into their natural habitat, but most zoo-animals will stay in captivity. However, those animals that will be released are probably not equal to their wild counterparts due to changes in behavioural traits (Kleiman et al., 2010). In attempts to reintroduce the endangered European mink (*Mustela lutreola*) in Estonia, 172 minks were released (Maran et al., 2009). The mortality was about 50 % during 1-1,5 months after release but then stabilized, and 75 % of the recorded deaths were caused by predators. This was much higher than the normal mortality rate, even though the wild European mink is considered to have a high mortality rate of both young and adults (Maran, 2003). The mortality of juveniles younger than one month can even be 36,8%. Other reintroductions have similarly been unsuccessful because of individuals being killed by predators, for example attempts in reintroducing captive-born greater rheas (*Rhea Americana*) (de Azevedo & Young, 2006).

Bremner-Harrison et al. (2004) studied variation in boldness in captive-bred swift fox (*Vulpes velox*) by exposing them to novel stimuli and then divided foxes into two groups depending on if they were characterized as bold or cautious. Later 31 juveniles were selected for reintroduction, but only 16 were radio-collared and followed. Six months after release the survival rate was investigated and the results showed that individuals that were judged as bold were most likely to die. In captivity when these individuals were exposed to novel stimuli, they had left their dens more quickly, approached more closely to the stimuli and shown more activities indicating low fear compared with those which survived. Bold individuals should thereby be less likely to avoid predators, conspecifics or anthropogenic stimuli that may pose a threat in the wild.

The reason that reintroductions are problematic is mostly because of the released animals being born in captivity and having developed in an unnatural environment (Kleiman et al., 2010). There is also a risk that animals in captivity have been habituated to stimuli that imply danger in the wild and there could be a selection for reduced fearfulness (Bremner-Harrison et al., 2004). Mortality will then be high in released populations because of individuals not exhibiting behaviours that are adapted for the wild environment (Kleiman et al., 2010). Therefore, introducing endangered species into the wild include a lot of planning. When training the animals for reintroduction several areas of behaviour have to

be considered and predator-avoidance being one of them (Kleiman, 1989). Captive-animals that are going to be released are often exposed to potential predators in hope for having higher survival rates in the wild (Griffin et al., 2000).

Shier & Owings (2006) trained juvenile black-tailed prairie dogs (*Cynomys ludovicianus*) to respond with anti-predator behaviour when predators were presented. After two weeks of training, the prairie dogs were released into the wild together with the non-predator trained control group. The survival success was controlled one year later and the results revealed that trained juveniles showed higher survival after release than untrained juveniles. Later on Shier & Owings (2007) studied if there were a difference between juveniles that had been trained with a demonstrator and juveniles that had been trained without a demonstrator and if there were a difference in survival between the groups. The results showed that the juveniles that had been trained with demonstrator had a higher survival rate than control group. This indicates that social transmission of anti-predator behaviour during training is a benefit and increases the chance for animals to survive after release. Their survivorship was also compared with released wild-reared juveniles and there were no differences in survival rate. This indicates that using social training when learning animals to avoid predators can emulate experience acquired in the wild.

Van Heezik et al. (1999) made two attempts in training houbara bustards (*Chlamydotis [undulata] macqueenii*) in predator-avoidance. Captive chicks in different groups were hand-reared with minimal human contact and hand-reared with intensive human contact but also predator-trained. During trainings a model of a fox with wheels was manipulated from outside and burst into the pen and lunged at the birds for one minute. During training alarm calls of wild adult houbara was also played. But this was not effective in improving survival after reintroduction and the group with minimal human contact did not improve survival either. In another experiment van Heezik et al. (1999) used a controlled hand-reared fox in the test cage at dusk or dawn. The fox watched, stalked, pursued and sometimes caught the houbara. There were also two wild-caught adult houbara in the group in hope for learning from observing conspecifics of natural responses. Playbacks of alarm calls were also played. After reintroduction there was a significant improvement in survival of the birds. Van Heezik et al. (1999) think that by using a live fox and providing an experience where the birds learned decision rules, might have given them a benefit and ability to shape future anti-predator responses. But because of injuring the birds during trainings it might be an unethical way of training. However, van Heezik et al. (1999) did not take the two wild-caught birds in consideration when analyzing and did not make a conclusion about social learning.

5.4. Enrichment and training

According to Rabin (2003) natural behaviour management programs should be incorporated into captive management programs at zoos in order to increase captive population's future survival and viability in reintroductions. How to manage behaviours should be planned and considered before reintroductions. It is important to establish which anti-predator behaviours each individual express towards specific predators (Watters & Meehan, 2006). There might be differences between individuals and species how they respond to the same predator (Stapley & Keogh, 2004). It would also be more effective if behavioural management was conducted regularly during all stages of a population's time

in captivity (Rabin 2003). Animals must be surrounded by appropriate stimuli early in development for proper behaviours to be developed. When planning enrichments the natural and individual history of an animal must be considered and plans should also include measurable goals and results (Mellen & McPhee, 2001).

There have been a lot of studies about anti-predator behaviour in captivity using artificial predators and playback of sounds. Blumstein et al. (2000) made predators that had a realistic look and presented them for tamar wallabies to study anti-predator behaviour. Acoustic treatments were also used which were sounds of conspecific anti-predator alarm, eagle calls and howls from dingoes. Beani and Dessí-Fulgheri (1998) studied defensive behaviour of Grey partridges (*Perdix perdix*) and simulated the presence of predators by using an aerial silhouette of a raptor, sounds of calls of raptors and alarms by other partridges. Habituation was considered and to avoid this, stimuli was varied and trials were placed at intervals. The study revealed that partridges showed strong responses to silhouette, but not call of raptors. However, partridges showed responses to alarm calls, but this might be because of the greater danger it represented. Sounds of a raptor that was out of view represented perhaps a lesser dangerous situation and raptors are also most often silent when hunting (Beani & Dessí-Fulgheri, 1998).

Masataka (1993) studied three groups of adult female squirrel monkeys (*Saimiri sciureus*) and tested fear response to real, toy and model snakes. In the first group the animals had lived at least two years in the wild before being captured and eight year in captivity, and in the second group the animals were laboratory-reared. The animals in the third group were also born in laboratory, but differed from the other two groups in getting live insects in addition with food. The results showed that wild-born animals and laboratory-reared animals fed with insects responded strongly to presentation of snake-like objects. The animals which were born in laboratory but not fed with insects, did not respond fearfully to the same objects. This indicate that even though squirrel monkeys do not have any experience of snakes, it can be sensitized a fear of snakes in experiencing small live insects. Being presented to reactive stimuli during development could according to Rabin (2003) act as a releasing mechanism for anti-predator responses. This could be perhaps be substituted for actual exposure to predators in natural behaviour programs and apply for other species too.

5.4.1. Training with unconditioned stimuli

Pre-training captive-animals have become common in reintroductions. Miller et al. (1990) studied how anti-predator behaviour developed and was expressed in captive-raised Siberian polecats (*Mustela eversmanni*) using the predator models badger and owl in mild aversive conditioning. The purpose was to study an ecological and morphological equivalent to the endangered black-footed ferret (*Mustela nigripes*) which at age two months appear above ground with mothers and at age four months spread out. Therefore, three different groups, classified in the ages two, three and four months, were studied. The results were that older polecats had quicker responses and learned in short-term to avoid predators. Miller et al. (1990) also believe that if the aversive stimulus would have been harsh or repeated enough the polecats might have learned avoidance in long-term. According to Griffin et al. (2000) unconditioned stimuli must have the same effect as that of a natural predator to be effective. Then a mildly unpleasant stimulus is not enough

because it does not represent a predator event. Startling stimulus is not effective either because it elicit only a temporary orient response.

McLean et al. (2000) tried to condition fear responses by two wallaby species, rufous bettongs (*Aepyprymnus rufescens*) and quokkas (*Setonix brachyurus*), to different objects. Half the population of rufous bettongs in the study were wild-caught and half were born in captivity. The animals that had lived in the wild had experience of dingoes, dogs and possibly foxes. The quokkas were captive-bred and had experience of sound and smell of dogs. But none of the two studied species had regular physical or visual contact with any type of canid. During tests McLean et al. (2000) presented a stuffed fox, a real dog or odours in the evenings when the wallabies became active. When the training part began, strings were used to get the fox-model to jump around and then the dog was let in. The dog had been trained to chase wallabies without injuring them. The fox was also used in training quokkas and this was carried out by one person chasing the animals with the fox suspended in front from a pole. The quokkas were afraid of humans due to capturing for management, and the purpose with the training was to generalise fear of humans to the fox. However, this was unsuccessful and quokkas did not become afraid of the stuffed fox. Training with odours was not successful either. But the results showed that quokkas generalised long-term fear from the dog to the fox and bettongs too responded fearfully towards the fox after trainings. Expressed anti-predator behaviours were increased vigilance, less feeding and moving to the back of the pen. It might thereby be possible to learn animals to recognize predators through linking an unreal predator and a similar live attacker (McLean et al., 2000).

De Avezedo & Young (2006) trained zoo-borned greater rhea using a model of a jaguar with wheels and a live dog. The animals were exposed to stimuli seconds before a human carrying a net entered and began a simulated capture procedure by chasing the birds without catching them. After the aversive experience was done and the human had exited the area, the stimulus was passed through view of the birds again. Control animals were only exposed to a chair on a wagon. The results were that training trials with the dog increased vigilance and defence behaviours but trials with the jaguar model gave more effectiveness. Reasons for this might be that it was difficult for the bird to see the dog which was black, or because domestic dogs are not their natural predators. Another interesting result is that there was no difference between training sessions; birds responded in the same way during all trials. The rheas had been isolated from predators in two generations and this result indicates that the time was not sufficient to eliminate all species-specific defence reactions.

Prairie dogs have many predators and Shier & Owings (2006) trained young prairie dogs with a moving model hawk, live ferret and live snake together with different sounds. Alarm calls of prairie dogs for recognizing mammals and avian predators are repetitiously barking in order to alert offspring. When the adult prairie dog sees a snake it approaches, sniff and jump away while barking (“jump-yipping”). In the study tests using a moving hawk or live ferret were combined with playbacks of alarm barking and tests with the snake were combined with playbacks of “jump-yipping”. The live predators and the prairie dogs were separated with mesh barriers. The results showed that juveniles exposed to the predators performed more anti-predator behaviour than untrained juveniles and the training had a lasting effect because the juveniles spent more time vigilant during the second trial compared to the first.

5.5. Welfare in captivity and ethical considerations for predator enrichments

The most important principles in animal welfare originate from “the Five Freedoms”, established by Farm Animal Welfare Council (FAWC):

- “1. freedom from hunger and thirst – by ready access to fresh water and a diet designed to maintain full health and vigour
2. freedom from discomfort – by the provision of an appropriate environment including shelter and a comfortable resting area
3. freedom from pain, injury or disease – by prevention or through rapid diagnosis and treatment;
4. freedom to express normal behaviour – by the provision of sufficient space, proper facilities and company of the animal's own kind
5. freedom from fear and distress – by the assurance of conditions that avoid mental suffering.”

According to FAWC the freedoms do not define standards for acceptable welfare but define ideal states and every animal should be considered. Then it will be ethical issues with natural behaviour management programs and managing behaviours that include stress. For preserving anti-predator behaviours, animals are exposed to aversive stimuli for preparing reintroductions (Rabin, 2003). The welfare of individuals will then be reduced, but the survival for reintroduced populations will be enhanced. One of WAZA's principles of Code of Ethics and Animal Welfare is that the aim of all members of the profession must be assisting in achieving the conservation and survival of species. But even though zoos should work for conservation and high ideals of species survival, the welfare of individual animals is not supposed to be compromised (WAZA).

To determine animal welfare, the behaviour, physiology and physical health of individual animals have to be analyzed (Kleiman et al., 2010). Species and populations differ in how they react on provocative interaction and thereby one animal might become stressed while another is not (Stankowich, 2008). The biggest danger is to be exposed to chronic, long-term stress because there will be a prolonged elevation of glucocorticoids that damage areas of the brain and reduce mental performance (Matteri et al., 2000; Morgan & Tromborg, 2007). For animals in captivity the greatest stressors are probably situations that the animal cannot control and escape from. The more an animal must cope when it is not being able to cope, the more is its welfare impaired (Kleiman et al., 2010). Control, choice and decision making are biological needs that are important, because it is something that animals are able to do regularly in the wild.

Growth and reproduction are not essential functions and will be inhibited by endocrine responses to stress in favour of maintenance and survival (Moberg, 2000). Acute responses are of importance because it has adaptive functions and is vital for coping and surviving. According to Kleiman et al. (2010) may some exposure to stress be good for animal well-being. This because of animals in the wild can be helped by stress to build a capacity to cope with environments. Stress in captivity can be similar in frequency, quality and

magnitude to the stress in the wild, but there are also several artificial stressors that captive animals are being put through, like limited space.

6. Discussion

The purpose of this study was to investigate if there is a need for captive animals to be enriched with predators and the possibilities for developing enrichments. If anti-predatory behaviour would be important for an animal in captivity, it could perhaps be called a behavioural need. I have not come to the conclusion that the prey-predator interaction is important for the individual captive prey animal, nor can I conclude that it is not. Anti-predator behaviours and responding to stimuli include a lot of physiological responses that perhaps could be of importance in some way. Prey-animals in the wild must also maintain a balance between intaking energy and fleeing from predators (Lima, 1998; Stankowich, 2008) but animals in zoos do not have to search for food or worry about predators. Maybe there are some physiological and psychical benefits in trying to maintain homeostasis and thereby it could be benefits to enrich zoo animals with predators too. Stress responses might even be good for the animal's well-being because of acute responses helping animal to build a capacity to cope with environments (Kleiman et al., 2010).

Anti-predatory behaviours might change when being isolated from predators (Blumstein & Daniel, 2003; McPhee, 2003; Blumstein & Daniel, 2005). Drawing conclusions about behaviours in captivity might be possible from studies about animals which are naturally isolated from some or all predators. Anti-predatory behaviours will probably be lost due to isolation from predators, especially those behaviours that rely on experience (Blumstein, 2002). For how long animals have been isolated seems to not affect predatory recognition either (Blumstein et al., 2004) and therefore maybe behaviours might become lost rather quickly in generations. Then one problem with releasing captive-bred animals into the wild is that they do not know how to avoid predators.

But training animals before releasing them in reintroductions have shown that those animals have higher survival rates compared to untrained animals after being released (van Heezik et al., 1999; Shier & Owings, 2006; Shier & Owings, 2007). It is important to plan carefully and train the animals in predator recognition and avoidance. Because of the animals often being endangered and having a high value, every aspect for their survival is crucial. The issue is perhaps how animals will be prepared for challenges they will come across in the wild. For teaching animals to avoid predators it may be necessary to use stimuli that have the same effect as a natural predator (Griffin et al., 2000). I guess that training with frightening stimuli is very stressful for an animal, but perhaps it is necessary for the animals to survive in the wild. But I feel that social learning should be more investigated and could be a good approach in training animals. Some juveniles learn about predators from their parents and rearing affects finetuning of responses (Beani & Dessí-Fulgheri, 1998; Griffin et al., 2000). Therefore it would be natural for a juvenile to learn from an adult. There could perhaps be problems in getting animals that are experienced and one alternative is to use wild-captured animals. This could be the best way to learn prey animals because of wild-captured animals being experienced with the real predators. But capturing animals might not always be possible because of the species being endangered or ethical issues. Then the captive-born demonstrator must be trained with frightening stimuli.

Enrichments can be used for reducing unnatural behaviours and increased animal welfare (Mellen & McPhee, 2001) or natural behaviour management for attempting to keep all components of a species' expressed behaviours in appropriate contexts (Rabin, 2003). According to Rabin (2003) more focus should be on keeping and promoting natural behaviours and behavioural programs should be managed for captive animals in order for them to behave as their wild conspecifics. I think there is a need for research about exposing animals in captivity with predator-models. It would be interesting to compare the survival rate of reintroduced animals that have been trained, with reintroduced animals that both been trained and whose ancestors have been exposed to predator models through generations. The only study I have found about anti-predator behaviours in captivity and behavioural changes in generations is the study by McPhee (2003) on wild caught oldfield mice, therefore more research is needed in this area too. I think that knowing about changes in behaviour is essential for conservation of endangered animals and especially for the specific animals that are planned for reintroduction.

I do not think it is necessary to condition anti-predatory responses for animals that are not going to be released, and I do not think it would be possible considering welfare. However, it may be a good idea to use predator-models for enriching captive animals and promoting natural behaviours. Especially considering that it is enough for a prey-animal to have one predator in its natural environment in order to respond to novel predators (Blumstein, 2000). Enrichments should be carefully planned for the individual animal (Mellen & McPhee, 2001) and should also be species-specific. I think it is important to have in mind what kind of animal it is, which predators it has and which anti-predator behaviours it express. Studies where anti-predator behaviour have been studied and trainings of animals in reintroductions could perhaps work as guidelines for developing enrichments or natural behaviours programs. Models and silhouettes of predators, odours of predators and playbacks of alarm calls and predator sounds could be used. The study by Masataka (1993) where squirrel monkeys that were fed with live insects responded to snake-like objects, could also be considered as a guideline for alternative anti-predator enrichments without exposing animals to predators.

But using visual enrichments might be better than using acoustic and odour cues. Because of the similar features that are shared by predators (Blumstein et al., 2000) prey-animals seem to have an integrated predator recognition system (Blumstein, 2006). Therefore it might be more likely that animals in captivity can recognize visual cues. According to Blumstein (2002) predator recognition by sounds and odours is based on experience, but according to Buchanan-Smith (1993) discrimination between predator and non-predator scents may be innate. Using sounds and odours could perhaps have lesser effects than visual stimuli. However, I think that playbacks and sounds of alarm calls and signals from conspecifics might be useful for enrichments and might for example increase vigilance in prey-animals. Because of it is important to avoid the animals to get habituated to stimuli it could be an idea to use different types of enrichments. Animals that become habituated may become bolder and there could be a selection for reduced fearfulness that have disadvantages for reintroductions (Bremner-Harrison et al., 2004).

Not exposing animals to frightening stimuli too often could also have a welfare perspective. If stimuli seem to be too stressful and frightening for an animal, I believe that the enrichment should not be continued considering the principle of FAWC that an animal should be free from fear and distress. It is also important to have in mind that individuals

are different and deal with stress individually (Stankowich, 2008) thereby one animal in a group might become more stressed than the other animals. It is also important to design closures in a way so animals can hide and get away from frightful stimuli (Mellen & McPhee, 2001). Not being able to cope with the situation means that the animal's welfare is impaired and long-term stress is also damaging for the animal. However, because of anti-predator behaviours might be lost in captive animals and animals isolated from all predators do not recognize predators as well as wild prey animals do, I believe that captive animals will not become too stressed when exposed to artificial predators.

7. Conclusions

I have not come to a conclusion if prey-predator interaction is important for the prey and prey animal in captivity, but I think that there is a need for enriching prey-animals with predators. Anti-predator behaviours of captive animals can change in generations and therefore anti-predator behaviour is important to consider when reintroducing captive-bred animals. Before releasing animals into the wild, animals can be trained by simple conditioning. Experienced demonstrators also enhance unexperienced juveniles' learning about predators. These juveniles have also better survival rates than trained without demonstrator and untrained captive animals in reintroductions. I think it would be possible to enrich zoo-animals with predator models, sounds and odours without affecting welfare negatively.

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