Czech University of Life Science Prague

Faculty of Tropical AgriSciences

Department of Animal Science and Food Processing in Tropics



Response of Cattle grazing on Pasture on olfactory Stimuli

Diploma Thesis

Author:

Bc. Kateřina Fiebigerová

Thesis Supervisor:

doc. RNDr. Pavla Hejcmanová, Ph.D.

Thesis Consultant:

Ing. Kateřina Hozdecká

Prague 2014

Affirmation

I declare that I am the only author of this diploma thesis "Response of cattle grazing on pasture on olfactory stimuli". I used only sources mentioned in references. I agree if this diploma thesis was saved in CULS library in Prague and this thesis will make accessible to study purpose.

In Prague dated 17th April 2014

.....

Bc. Kateřina Fiebigerová

Acknowledgement

I would like to thank my thesis supervisor doc. RNDr. Pavla Hejcmanová, Ph.D. for her large support and thoughtful leading and inspiring of this work. I would also like to thank my thesis consultant Ing. Kateřina Hozdecká who was always willing to answer my questions and she helped me when I was cornered. And big thanks to my family for their support and understanding. Mainly to my little daughter who slept and did not cry when I was working.

Abstract

This diploma thesis is focused on responses of cattle on olfactory stimuli. The investigation was conducted on Experimental Station for Fodder Production, Animal Nutrition and Dairy Science -Gut Grunschweige, Eiting, Germany, belonging to Munich Technican University. Animals were bred in farm conditions on pasture and there were observed 2 herds of Limousine cattle. The objective of this paper was to determine whether cattle respond to different smells in terms of motivation conflict between grazing and antipredatory behaviour. There were used four types of scent samples - control sample, smell of wolf (sympatric predator), African wild dog (allopatric predator) and eucalyptus oil (as neutral olfactory stimulus) which were installed to the mineral lick construction. There were collected a total of 3,366 records of entries to the licking area and 1,262 entries to the licking area during the experiment. There were found significant differences in frequency of occurrence of cattle in the licking area. Control sample was more frequented than samples with all three another scents. The highest frequency was recorded when there was not any sample. In general, cattle spent significantly more time in case when control sample was present before and after this experiment. There was not significant difference in time which was spent in control area with concrete odour. There were quit significant differences between total time spent in licking area weight of individuals.

Key words: antipredator behaviour, ungulates, predation risk, olfactory stimuli, olfaction

Anotace

Tato diplomová práce pojednává o reakcích skotu na čichové stimuly. Výzkum byl prováděn v Experimentální stanici pro produkci krmiv, výživy zvířat a mléčné užitkovosti – GUT Grunsweigne, Eiting, v Německu. Spadající pod Technickou univerzitu v Mnichově. Zvířata byla chována na pastvě a pozorována byla dvě stáda limousinského skotu. Cílem práce bylo zjistit, zda vůbec a případně jak skot reaguje na různé pachy z hlediska motivačního konfliktu mezi krmením se a antipredačním chováním. Byly použity čtyři pachové vzorky – kontrolní vzorek, pach vlka (původní predátor), pach psa hyenovitého (nepůvodní predátor) a eukalyptový olej (jako neutrální vzorek). Pachové stimuly byly připevněny na konstrukci u minerálního lizu. V průběhu experimentu bylo zaznamenáno 3366 vstupů do oblasti s minerálním lizem. Byly nalezeny signifikantní rozdíly ve frekvenci výskytu skotu v místě s minerálním lizem. Kontrolní vzorek byl navštěvován častěji než zbylé tři s pachem. Nejvyšší četnost byla zaznamenána, když v místě s lizem nebyl žádný vzorek. Obecně skot trávil signifikantně více času v místě s lizem, když byl přítomen kontrolní vzorek a před a po tomto experimentu. Rozdíl v čase, který zvířata strávila v oblasti s lizem s konkrétním pachem, nebyl potvrzen. Ale vliv váhy na celkový čas strávený v místě s lizem signifikantně potvrzen byl.

Klíčová slova: antipredační chování, kopytníci, predace, čichové podněty, čich

Content

1		INTRODUCTION	1 -
	1.1	Motivation conflict	2-
	1.2	2 Predation risk	2-
]	1.2.1 Reduction of predation risks	3 -
	1.3	3 Antipredator behaviour	4-
]	1.3.1 Types of antipredator behaviour	5 -
	1.4	Sex dependence on antipredator behaviour	- 12 -
	1.5	5 Age	- 15 -
	1.6	5 Prey-predator interactions	- 15 -
]	1.6.1 The role of the time	- 17 -
	1.7	7 Role of original predator	- 17 -
	1.8	B Domestication and its influence on antipredator behaviour	- 18 -
	1	1.8.1 Reduction of antipredator behaviour	- 18 -
	1	1.8.2 Antipredator behaviour of domesticated animals	- 18 -
2		THE AIMS OF THIS THESIS	- 20 -
3		MATERIALS AND METHODS	- 21 -
	3.1	Study area and investigated animals	- 21 -
	3.2	2 Data collection	- 22 -
	3.3	3 Statistical analyses	- 24 -
4		RESULTS	- 25 -
	4.1	Pasture K6	- 25 -
	4.2	2 Pasture K8	- 30 -
	4.3	3 Difference within pastures K6 and K8	- 32 -
5		DISCUSSION	- 34 -
6		CONCLUSION	- 37 -
7		REFERENCIES	- 38 -

List of Tables

Table 1 List of observed animals from pasture K6 and K8
Table 2 Frequency of cattle occurrence of cattle in licking area during scent presence in pasture K6 25 -
Table 3 Frequency of occurrence of each individual in licking area in pasture K6 during experiment - 25 -
Table 4 Frequency of cattle occurrence in licking area during scent presence in pasture K8 30 -
Table 5 Frequency and mean time of entries to the mineral lick according type of odours 33 -

List of Figures

Figure 1 Percent of time (x \pm SE) adult female cattle exhibited vigilance during peak foraging hours in relation to group size. Group size were 1-5 animals (n=32), 6-20 animals (n=98), or >20 animals (n=84) (Kluever *et al.*, 2008).....-7 -

Figure 2 The influence of social status (mother, adult female without calf, yearling, male) and encounter risk (high back; intermediate shaded; low white) on (a) mean \pm SE scan duration (s) and (b) mean \pm SE scan frequency, number of scans (min) of focal individuals (Childres and Lung, 2003)....-13 -

Figure 3 Time spent scanning (a), average scan duration (b) and scan frequency (c) as a function of group size and sex in Przewalski's gazelle *Procapra przewalski* (square: female; triangles: male; diamonds: mother) (Li *et al.*, 2009)....-14 -

Figure 4 Proportion of bulls among reindeer killed by lynx Lynx lynx in northern Scandinavia in 2006-2011 separated by male and female lynx and the age of reindeer. The grey polygon represents the range of reported bull proportions (adults only) in winter herd among relevant reindeer districts, the striped line shows the expected proportion of males among newborn calves, and error bars are Clopper-Pearson 95% confidence intervals (CIs). A lower CI above the reported range implies selection for bulls/male calves by the lynx (Mattison *et al.*, 2014)....-15 -

Figure 5 Pathways by which predation can affect the population dynamic of prey: the restricted view that predation operates only through direct offtake is illustrated by two orange arrows linking predation rates to prey dynamics by way of survival; this is only the tip of the iceberg. Pink boxes and arrows illustrated that direct predation rates are not simply an external ecological force imposed on prey by predators, but are determined jointly by the intensity of predation pressure and the antipredator response of prey to that pressure. This creates a feedback loop between direct predation and antipredator responses. In turn, antipredator responses can have physiological or energetic costs for prey, which could alter prey dynamics via either reproduction or survival. These risk effects are illustrated by blue arrows, with likely feedbacks illustrated by gray arrows (Creel and Christianson, 2008).- 16 -

Figure 13 Dependency of weight on frequency and total time of occurrence in licking area in pasture K6: a) real frequency data, b) log ₁₀ transformed data 30 -
Figure 14 Total time spent in licking area on pasture K8 31 -
Figure 15 Dependency of weight on frequency and total time of occurrence in licking area in pasture K8: a) real frequency data, b) \log_{10} transformed data
Figure 16 Total time spent in licking areas on pastures K6 and K8 32 -

1 INTRODUCTION

The predation is one of the most important forces of the natural selection and it is one of the factors which may have strongly affected an evolution of animal behaviour (Abrahams and Dill, 1989; Lima and Dill, 1990; Childress and Lung, 2003; Jones and Godin, 2010). There exist two predation effects of a prey. The first one is direct effect which causes death of the prey. This effect may have influence on population size. The second and more important one is indirect effect when the prey is exposed to a predator but it is not killed. This indirect and non lethal effect strongly affects animal lifespan (Creel and Christianson, 2007). The indirect effect of predator may affect the fitness of its prey. These animals are under predation pressure and they are stressed. And it may have greater impact on their behaviour, reproduction success and others behavioural mechanism of preys (Lima and Dill, 1990; Candolin, 1997; Lima, 1998; Apfelbach et al., 2005; Creel and Christianson, 2008; Vijayan et al., 2012). Animals often have to choose if they will be careful and they will just control their environment or they will risk and they will devote to other activities such as foraging, matting and other activities (Dumont and Boissy, 2000; Corlatti *et al.*, 2013). So that animals have learned how to reduce this risk by antipredator behaviour. This strategy consists of various types of behaviours. The most important for ungulates is vigilance which may help them to recognize dangerous situation (Hunter and Skinner, 1998). Then alarm calls which may alert other conspecifics, inform predator that it was revealed or it allows immediate escape (Caro et al., 2004; Stevensen et al., 2008). Reactions of animals are different according natural predators and to allopatric predator. Behavioural response to native predator is often much significant because of long time coexistence and stronger predation risk. (Apfelbach et al., 2005; Parson et al., 2007; Christensen and Rudgren, 2008; Navarro-Castilla and Barja, 2014). So animals could adapt to presence of predator (Apfelbach et al., 2005). And these adaptations may help them to survive predator's attack and/or avoid it (Christensen and Rundgren, 2008). It was described that some antipredator behaviour may be innate (Murray et al., 2004; Blumstein, 2006; Gall and Mathis, 2010). But domestication has huge influence on this behaviour. Animals are selected to be calmer, less fearful (Cornelia and Temple, 2013) and it may cause reduction of antipredator behaviour because of increases fearfulness. Domesticated animals may have longer immediate reaction to predator in contrast with wild animals (Muhly et al., 2010; Laporte et al., 2010). Anyway these animals have not met predator for long time and many generations.

1.1 Motivation conflict

Animals often have to choose between feeding and others social motivations (Bailey et al., 1996; Dumont and Boissy, 2000). It means that ungulates should optimize its decisions in terms of proportion of time spent by different activities and energy output. One of the most important activities not only for ungulates is feeding because it may ensure growth, reproduction and last but not least survival of individuals (Coralatti et al., 2013). There are several factors due to animals choose their pasture - these are slope and distance to water supply, forage quality, species composition and spatial memory (Bailey et al., 1996). It can help them to recognize relatively safe environment or pastures with really quality pasture because these two things often do not occur together (Kluever et al., 2009). Feeding related to several others behaviours. Dumont and Boissy (2000) concretly described that sheep may choose their feeding place by the strength of social bonds. Animals which are reared together have stronger bonds with each other and rather are subjected to group than to food. And on the other hand individuals in new group choose their favorite food and immediately select feeding instead of rest of herd. During the matting season it occurs while distribution of activities. Some males spent more time with foraging and others rather invest their energy to sexual interactions and try to increase the chance to mating (Coralatti et al., 2013). And naturally this conflict leads to predation risk when animal has to choose if it will try to defend itself or if will feed itself even at the cost of increased possibility of encounter with predator. Such as moose (Alces alces gigas) fed itself in a large group when it was at a greater distance from edge of forest. There is higher risk in open area and so moose browsed less selectively too (Dumont and Boissy, 2000). Many ungulates migrate to other habitat when predation pressure is high. These are for example reindeers (Rangifer tarandus fennicus and R. t. tarandus) (Kojola et al., 2004), elk (Cervus elaphus) (Hebblewhite and Merrill, 2009).

1.2 Predation risk

Predation risk has strong influence on each animal. Predation risk is a factor which affects lots of behaviours such as mating behaviour. Animals living under high predation risk show lower breeding success in contrast with animals living in areas with low predation risk. Females have not such need to mate and they have reduced interest in males (Evans *et al.*, 2002). Males often reduce their agonistic interaction with other males when predation risk increases (Kelly and Godin, 2001). Females may have a higher rate of abortion, infants are weakened and litter contains less offspring. Better forage is usually in places with more predators (Navarro-Castilla and Barja, 2014). So animals try to avoid them by choosing another habitat even at the cost of being disadvantaged. Because animals may choose habitat on the edge of territory of the predator

due to possibility of predation is higher in places where territories of predator and its prey are overlap. This is related to changing of animals foraging patterns. They are able to choose worse pasture at a price lower possibility to be attacked by predator. But animals feeding on unfamiliar pasture may have got a problem with malnutrition because of higher vigilance behaviour when they can not forage. Animals which do not know habitat where they present, they increase alertness. And lower food intake is in connection with this type of behaviour (Howery and DeLiberto, 2004). Group-living animals usually choose worse feeding in exchange to lower predation risk. But it compensated that animals consume worse feed composition. It can cause lowering of fitness due to low energy intake. Such as caribou females during calving season try to escape to mountains against wolf predation. They left lowlands with quality forage and change place for low energy intake as the price of less potential of predation of their calves. Navarro-Castilla and Barja (2014) found that wood mice (*Apodemus sylvaticus*) reduced food intake when they were under predation risk. It follows that living under predation risk is usually disadvantageous, animals adopt many types of antipredator behaviour which may reduce this antipredator pressure.

1.2.1 Reduction of predation risks

Immediate detection of predators is critical for animal which needs to avoid them. So animal may to recognize threats. If an individual can quickly determine dangerous situation it will quickly react. The recognition of predator in time can help to survive or escape (Devereux *et al.*, 2005). Each animal is dependent on its senses because senses help them to find feed, possibility to reproduce itself, protection against predators and others. Their senses may help them to immediately detect danger and react quickly. As I mentioned, through the senses animals can distinguish possible predation risk. The vision, audition and olfaction are the most important senses for them in this case. Using of these senses varies according to diverse habitats. Ungulates living on the plains need mainly vision and olfaction and ungulates living in dense forest use audition and olfaction. These senses help them to recognize potential hazards as quickly as possible.

One of the main senses is the olfaction. The olfaction is the dominant sense for most mammals (Ache and Young, 2005; Brennan *et al.*, 2006). It is chemosensory ability of terrestrial mammals for detection of low concentration of airborne, volatile chemical substances. Odours can help animals to find essential needs as water, food, etc. and avoid a danger such as predator or natural hazards as fire (Ache and Young, 2005). We know that ungulates in the wilds have this sense really developed. It depends on all-day using. When individuals smell odour of predator which

can be potential threat, the olfaction can alert them (Parsons et al., 2007). But it is not only used for detection of predator but it can help to recognize other animals. E.g. during estrus cycle the urine of females of black-tailed deer is strong attractant for males (Müller-Schwarze, 1974). With olfaction relates scent marking. Most carnivores are territorial so they use secretion of urine, faeces and scent glands to their territory (Navarro-Castilla and Barja, 2014). And the animals can use it in alarming situation such as passing dog or entry to unknown area (blacktailed deer) (Müller-Schwarze, 1974). Or when animals see unfamiliar individual of the same sex or they are in frightening/stressed situation (as Maxwell's duiker) or just to marked new objects (as zebras) (Rails, 1974). White-tailed deer marks or delineates its area (Moor and Marchington, 1974). This behaviour can warn or inform other animals. It follows that the role of odours is really important for many animals. Laboratory rats can identify stress in urine of their conspecifics and they can evade to risky area. Cattle react to faecal odour of predator but it is just a demonstration of reduction of food intake (Terlouw et al., 1998). Hedgehogs (Erinaceus europaeus) reacted strongly to their natural predator badger (Meles meles). The odor of the predator was given to the area of hedgehogs. They avoided it and refused to forage there. This risk disappeared four days after and hedgehogs start to feed in this area again (Apfelbach et al., 2005). Christensen et al. (2005) found that visual, olfactory and auditory novel stimuli reduced eating time of horses. These all increased heart rate. It means that these stimuli could cause feeling of danger. Rising of heart rate prepares the body to escape from predator or just from possible dangerous area. Olfactory stimuli do not cause increasing of heart rate but cause increasing of sniffing and interrupt feeding. Low reaction of horses to olfactory stimuli could be caused by slow transfer of these stimuli by air and these do not bring so high probability of danger that waiting is better strategy than impetuous flight. Olfactory stimuli increased horse vigilance and lower food intake. It means that these stimuli are very important and can bring some potential hazards.

1.3 Antipredator behaviour

Predation risk can be lower by special types of behaviour called antipredator behaviour. These behaviours can decrease probability of contact with predator. And when animal meets the predator, these can help it to survive this encounter or escape with minimum losses. Animals may use behaviour of primary defense as avoiding predator. E.g. living in herds in ungulates or using inconspicuous coloring. Secondary defense is antipredator behaviour which is used when predator is present. This is flight reaction in ungulates for example (Apfelbach *et al.*, 2005). Predators have ability to recognize more vulnerable prey in the herd of ungulates. This can help them to hunt with higher success. Often alpha individual from the pack of predators attacks.

Ungulates can react to predator depending on which predator attacked them. It means that often dominant pack member leads an attack. Ungulates can decide which member of pack is more danger for them – they can recognize the most dangerous attacker. Gese (1999) wrote about this behavior, that herd of ungulates often behaves aggressively towards alpha coyote, because alpha dog leads the attack. So for herd it is easier to defuse originator than intimidate all pack. But it depends mainly on season because at the summer calves are presented in the group and females take care of them. Consequently females have more aggressive behaviour in this time. Immediate reaction may save them against attack of predator. Antipredator behaviour changes during a life of animals due to many factors. Lingle et al. (2008) said that young ungulates are more aggressive than older. It is related to antipredator technique because young animals have to attack the predator and have to be more aggressive so that they may survive an encounter with predator. Older animals are able to flight to the predator because their physical abilities are more developed. Some authors said that antipredator behaviour is innate and it is more important than learned behaviour. It is significant for survival of neonates. E.g. Young fawns can also learn how not to confront with predator from their mothers (Swanson et al., 2002). Choosing of place for living and feeding may decrease possibility of encounter with predator too. Therefore right selection of habitat can significantly reduce predation risk. There are habitats where possibility of encountering with predator is higher than elsewhere. These types of habitats are water holes, dense vegetation and others (Howery and DeLiberto, 2004). Hunter and Skinner (1998) wrote about vigilance of ungulates that in the thick cover animals are more vigilant than in open habitat. That means that possibility of predation is higher in dense vegetation. Animals can exploit different habitats for their own protection, so e.g. ungulate females with neonates use different environment by their antipredator strategy (Bongi et al., 2008).

1.3.1 Types of antipredator behaviour

The animals adopted many types of antipredator behaviours. Animal may defend against predator alone or in group. Self-defence is usually more difficult because individual has limited possibility of antipredator behaviour (Niemalä *et al.*, 2012). Animals living in group have many advantages in avoidance predator against animals which are living alone. Individuals may use auditory and visual signals which may help them to avoid a predator (Hoogland, 1979; LaGory, 1987; Caro *et al.*, 2004). And animal may react to predator defensively because this behaviour may save energy more than direct confrontation with predator (Lima and Dill, 1990). Vigilant behaviour may animals help to detect the predator (Hunter and Skinner, 1998). After that animal may react and safe itself. Other behaviours which are used after detection predator are alertness signals. These may warn conspecifics or predator that it is detected (Caro *et al.*, 2004)

(a) Vigilance and group size effect

Vigilance is a special type of animal behaviour which has many types of various reasons. The main reason is recognition of dangerous situation (Hunter and Skinner, 1998). Vigilant animal is characterised by raise head, open ears and by scanning of surroundings. In this case, animal stops various activity (e.g. feeding, lying, moving) until the risk situation is not away (Howery and DeLiberto, 2004), so vigilance brings some disadvantages. Because a lot of this behaviour has negative influence on animals. But vigilant behaviour can significantly help to animals. It is not related just with antipredator behaviour. It has also social function (Blumstein, 2006). The vigilance usually increases with increasing risk such as more hazardous time: It is time when predator may attack more frequently. Next vigilant behaviour increases with dangerous habitat and areas in group as periphery of this group (Howery and DeLiberto, 2004). But not always vigilance is higher with higher predation risk (Li et al., 2009). There are two types of vigilant behaviour. It is "social monitoring" when one animal watches behaviour of another animal in the group. And "antipredator vigilance" when animal is searching for predator. Both may decrease predator risk by immediate recognition of potential danger (Marino, 2012). Less vigilant animals are more vulnerable to predator attack. Animals which show high rate of vigilant behaviour often do not display other antipredator behaviours. Vigilance with low predation risk decreases but the size of group is still the same. It means that advantage of bigger group size has antipredator advantagous effect (Hunter and Skinner, 1998). Scanning rate increases after contact with predator. It may reduce probability of recurrent attack (Devereux et al., 2006). There are many factors which influence vigilance. Several of them are group size and sex (Li et al., 2009).

Group size has often negative relationship with vigilance. It means that animals may spend lot of time with other activities than scanning their environment. This is known as group-size effect and it is documented in many species (Fernández-Juricic *et al.*, 2007; Li *et al.*, 2009; Xu *et al.*, 2010; Marino, 2012). Vigilance is in relation with position of individual in a group. Animals on the edge are more vigilant than their companions in the middle because these are more exposed to attack (Hunter and Skinner, 1998). Position is important in other case also because animal interacts by its neighbor within group. It means when neighbor is vigilant animal starts to be vigilant also (Lima, 1995). This behaviour leads to faster detection of predator with less need to watch surrounding (Roberts, 1996). And so in herd or flock animals individuals can spend less time to vigilance and more time to foraging (Lima, 1995; Lima *et al.*, 1999; Robinette and Ha, 2001; Fernández-Juricic *et al.*, 2007; Li and Jiang, 2008). Individual vigilant behaviour decreases with increasing group size (Fig. 1) (Lima, 1995; Roberts, 1996; Reboreda and Fernandez, 1997; Fernández-Juricic *et al.*, 2007).

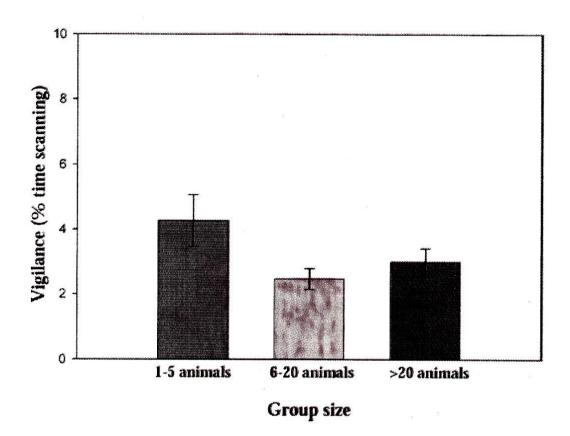


Figure 1 Percent of time (x \pm SE) adult female cattle exhibited vigilance during peak foraging hours in relation to group size. Group size were 1-5 animals (n=32), 6-20 animals (n=98), or >20 animals (n=84) (Kluever *et al.*, 2008)

This behaviour is typical for mammals, birds, and some fish species (Lima, 1995). But higher group size does not provide better detection of risks but it reduces the pressure to be vigilant and animals can spend time with other activities as feeding. The predator often attack larger groups than smaller. So why do animals search bigger group still when there is higher possibility of predation? It is explained that reduction of vigilance behaviour is more important than the probability of catching (Roberts, 1996). Hunter and Skinner (1998) found that ungulates which live under high predation pressure by lions have unexpectedly lower rate of vigilant behaviour. But they compensated decreased vigilance by other types of antipredator behaviour. These are active self-defense and grouping to extremely large herds. As mentioned above, the vigilance pressure is not so high in group and animals can spend a lot of time with other activities.

(b) Grouping

Individual often choose bigger group than smaller for living. Bigger group does not save it against predator but probability of attacking on this concrete individual is lower. The main

explanation of grouping in the connection with antipredator behaviour is protection against predator (Coster-Longman *et al.*, 2001). Grouping gives to animal lot of advantages. Group brings benefits for resource acquisition. Animals can forage themselves in more risky habitats when individual does not do it. E.g. larger group can forage in open habitats where possibility of predation is higher (Thaker *et al.*, 2010). It allows animals spend more time with foraging and ruminating (Howery and DeLiberto, 2004). Low density of group decreases competition for feed so animals can graze in safer habitats with worse forage. Meanwhile bigger group can help animals to reduce predation risk so they can use better grazing habitats with higher occurrence of predators. It means that animals may feed in smaller groups when forage is not so good and so ungulates may increase group size with better forage (Vijayan *et al.*, 2012). Animals may form groups only temporarily, such as seasonally (e.g. migration) and this can give them important benefits against predators (Messier, 1994). Detection of bigger group by predator is not lower but attack to concrete individual is reduced (Coster-Longman *et al.*, 2001). There are three hypotheses about mechanisms of Group size: "Many eyes hypothesis", "Safety in numbers" and "Scramble competition" (Xu *et al.*, 2010; Xu *et al.*, 2013).

"Many eyes hypothesis" is about advantage of group. There are more eyes scanning their environment for possible danger in group (Hunter and Skinner, 1998; Fernández-Juricic *et al.*, 2007; Laporte *et al.*, 2010). Bigger groups can detect predator sooner than smaller ones (Lima, 1995). The advantage of group is dilution effect of predator (Roberts, 1996; Thaker *et al.*, 2010). Because of higher number of group members decreases the individual risk of being predate because predator can often catch just the one prey at the one time (Frommen *et al.*, 2009; Turner and Pitcher, 1986). This leads to confusion of predator due to many possible targets. Because predator decides difficultly on which concrete prey it can attack and it may reduce risk of predation of individual. This effect is so significant for preyed animal that when individual has to choose group it chooses the bigger one (Frommen *et al.*, 2009). "Safety in numbers hypothesis" means strategy when individual is protected by a group. Because of predator may attack just one group member so possibility of attacking only one group member is greatly reduced. "Scramble competition hypothesis" is about competition for feed due to big group and reduced sources. Rate of vigilance decreases (Xu *et al.*, 2013).

(c) Alertness signals

Antipredator behaviour has signals which can show us that animal is restless. Every animal behaves differently when it is calm and when it is stressed. Ungulates use several auditory and visual signals which are using for communication in group and may show that there is something

wrong (Caro *et al.*, 2004; Stankowich, 2008). And these are used by animals for communication with conspecifics and also with predator (Alvarez, 1993; Caro *et al.*, 2004). These signals could be intentional or unintentional and are used after detection of predator. Alertness signals are commonly use in a group because they bring lot of benefits mainly for individual. Individual alertness is negatively correlated with group size. So animals are safer when they do not signal themselves. It does not attract the predator itself. It is in connection with concrete place in a group because the edge of community is often more dangerous than the middle of it (Hoogland, 1979).

Auditory signals

Auditory signals include snorting, whistling and foot stamping. These represent signals which are used mainly in group (Caro *et al.*, 2004). Colobus monkeys use snorts to inform their conspecifics about danger and they snorts mainly when they are confronted with predator (Schel *et al.*, 2009). White-tailed deer snorts when he sights predator. It has a function to warn a predator that it has been recognized by its possible prey. Snorting is more common in social living animals (with higher number of group members) (LaGory, 1987). Thomson's gazelles through the snorting inform predator about it detection. Whistling is more usual in close habitat where a bad visibility is. This signal is mainly for conspecifics but to a predator it may give information about its disclosure. Foot stamping is used mostly in open habitat where this distinctive and loud sound is clearly audible. But in dense vegetation food stamping may warn other conspecifics because it is harder to see predator (Caro *et al.*, 2004).

Alarm calls are other important auditory signals of animals. It is connected with some situation which could be dangerous. Alarm calling has dilution or confusion effect to predator and may decrease of probability of being attacked. This behaviour is not use always when predator is near. For example it is used in the Common Starlings in connection with long grass when other signals are not possible to use (Devereux *et al.*, 2008). White-faced capuchins use several types of alarm calls depending on type of danger. This allows to conspecifics quickly recognize what is coming (Digweed *et al.*, 2005). Lapwings (*Vanellus* spp.) use different types of alarm calls depending on the type of predator. The space whence predator may attack (air or ground) is for animals more important than class of predator (reptile, bird or mammal). But alarm calls could be false. This phenomenon was described by Evans *et al.* (2004) as a reduction of competition for feed.

Visual signals

Visual signals are mainly used just in the presence of predator. These signals are tail flicking and flagging, bounding, leaping and stotting, zigzagging, tacking and prancing (Caro *et al.*, 2004). Alvarez (1993) found that rate of tail flicking rises with increasing predation risk and it is used more towards predator than conspecifics. Tail flicking and flagging occurred more often during feeding and alert situation. But this behaviour does not always indicate danger situation (Stankowich, 2008). Tail flagging presumably does not warn conspecifics of the danger but this behaviour prevents to flight reaction against presence of predator (Caro et al., 1995). Tail flagging often use animal in good health condition so it suggest that predator may attack more vulnerable prey which is characterized by non flagging tail (Hirth and McCulough, 1977). Stotting has function to confuse predator and to signal it that ungulate is in a good condition and health. Stotting informs predator about it detection in Thomson's gazelles and neonate may inform its mother that it needs defense (Caro, 1986). Hirth and McCullough (1977) wrote about bounding and stotting behaviour that these behaviours are used mainly in noncritical situation when there is no direct attack of predator. Zigzagging, prancing and tacking are movement adaptation to escape to predator (Caro et al., 2004; Stevens et al., 2008). These adaptations allow a quick escape from the reach of predator by changing trajectory and speed (Stevens et al., 2008).

(d) Defensive reactions to predator

Defensive attack is used mainly by parents whho protect their offspring (Grovenburg *et al.*, 2009; Lingle *et al.*, 2005). And the type of habitat is not important. This behaviour is used identically in open and in dense habitats (Lingle *et al.*, 2005). This behaviour is energetically expensive so it is not used like the main antipredator tactic and animals choose it when they could lose a lot. It leads mainly with parental care. Ungulates are aggressive mainly to wild predators as wolves, coyotes, bobcats and bears but females may be aggressive towards males during parturition and after they may protect young against dominant males (Grovenburg *et al.*, 2009). Mule deer (*Odocoileus hemionus*) usually reacts aggressively towards coyotes. This may help them to survive coyotes' attack (Lingle and Pellis, 2002).

Place of feeding relates to how quickly can animal get to safety area. But how does animal risk possibility of predation in danger area with predators? Because not all encounter with predator leads to predation and decision to escape cost a lot of energy. So the main decision factor is how much animal wants to risk. Or if animal is able to get to safety area so quickly that predator can not catch it. Flight reaction belongs to defensive behaviour too. Ungulate may react to their

enemy by flight. The animal cover distance mainly depends on herd structure. Because females with youngs are more vulnerable they run longer distance because of protection of their offspring (Ciuti *et al.*, 2008). White-tailed deer (*Odocoileus virginianus*) normally flight against coyote and they use is as a primary antipredator tactic (Lingle and Pellis, 2002). Rate of escape depends on number of individuals too. The flight-initiation distance of large group is shorter than in smaller group. More cryptic individuals have longer flight-initiation because animals which are more visible to a predator have to have more quick reaction if they do not be eaten (Lima and Dill, 1990). Predation risk may be decreased by terrain choosing. The Finland reindeers (*Rangifer tarandus*) know how to avoid themselves to wolves predation. It means that wolves can not move so good in snow or on ice where reindeers do not have problems with moving. So reindeers chose soft or hard terrain to higher the possibility to lower of predation risk (Kojola *et al.*, 2004). Similar finding comes from Poland also. Local snow

hunting. When snow cover is not so deep wolves can hunt in creeks and ravines when it is impossible with deeper snow cover (Gula, 2004). But deep snow may not be always hunting disadvantage for wolves. Because killing rate of moose is higher when snow depth increases (Nelson and Mech, 1986). Wild ungulates generally choose worse food resources when predator is near (Muhly *et al.*, 2010). They want to avoid the possibility of predation so they choose forested habitat instead of open grasslands where better forage is presented (Morgantini and Hudson, 1985). Animals may stay inconspicuous by freezing behaviour. It means that ungulate stay on the same place without any movement. Cryptic coloration and dense vegetation may help it to be invisible so this behaviour is more often in rocky terrain and in forests because any enemy may overlook it. Body size is related with freezing too, smaller ungulates use it more often. Freezing is often in connection to hiding tactic of newborn ungulates (Caro *et al.*, 2004). This may reduce predation risk in newborn ungulates by combination of cryptic and immobility (Blumstein, 2006).)

(e) Antipredator strategies of mothers

This antipredator strategy of mothers concludes "hiding" and "following" strategies. The first uses close habitats. Mothers are present near to their lying offspring (Bongi *et al.*, 2008; Fisher *et al.*, 2002). Choosing of place for hiding is extremely relevant for neonates. But mothers choose these places mainly due to forage composition than due to predation risk. The hiding place must be minimally conspicuous so it is covered by dense vegetation (Ponzacchi *et al.*, 2010; Torriani *et al.*, 2006). Hiding strategy decreases probability of encounter with predator compared to following strategy when newborns are more vulnerable to attacking of predator (Lingle *et al.*, 2008). Mother should be so close to it in case she will intervene in the event of attack (Ponzacchi

et al., 2010). But mothers are at least 100 meters away from their neonates and they are returning mainly to suckle their offsprings (Fisher et al., 2002). Youngs which are using this hiding strategy are isolated from others ungulates. It is silent not to disclose itself to predator (Briefer and McElligott, 2011). Hiding tactic is usually changed when ungulate is older and it is able to flight to predator. Survival rate so rises steeply (Lingle et al., 2008). Ungulates which use this strategy are for example roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*) (Ponzacchi et al., 2010), fallow deer (*Dama dama*) (Torriani et al., 2006). The second is "following strategy" which uses open habitats to reduce of predator risks because youngs follow their mothers soon after birth (Fisher et al., 2002; Bongi et al., 2008). It means that neonates have to be mobile soon after birth so they may use defense of herd against predators (Torriani et al., 2006). But they are still close to their mother and they rarely move away from their mothers (Daleszczyk, 2004). Ungulates which are following are often bigger than ungulates which are hiding (Fisher et al., 2002). Following ungulates are e.g. Bisons (*Bison bison*) (Daleszczyk, 2004).

1.4 Sex dependence on antipredator behaviour

Generally valid, females and males have different life strategies (such as foraging and breeding strategies) (Li *et al.*, 2009). Females need to devote an energy to upbringing and survival of their offspring. Instead of, males have to fertilize as many females as possible. It follows that males have another antipredator strategy than females (Abrahams and Dill, 1989). So rate of vigilance is also different in males and in females (Xu *et al.*, 2010). Especially pregnant and lactating mammalian females have different behavioural patterns. These patterns are focused mainly to survival of their offspring (Fig. 2) (Bongi *et al.*, 2008). Because predators attack mainly offspring but indirect effect of it may hit their mothers by higher vigilant behaviour or choosing of another and often worse pasture. Bison cows (*Bison bison*) are more vigilant in habitat with wolves (*Canis lupus*) which are their predators (Howery and DeLiberto, 2004). Females and females with youngs are often more vigilant than males (Fig. 3) (Hunter and Skinner, 1998). Females use aggressive defence mainly when they have youngs. This behaviour can lower predation risk of their calves (Lingle *et al.*, 2008).

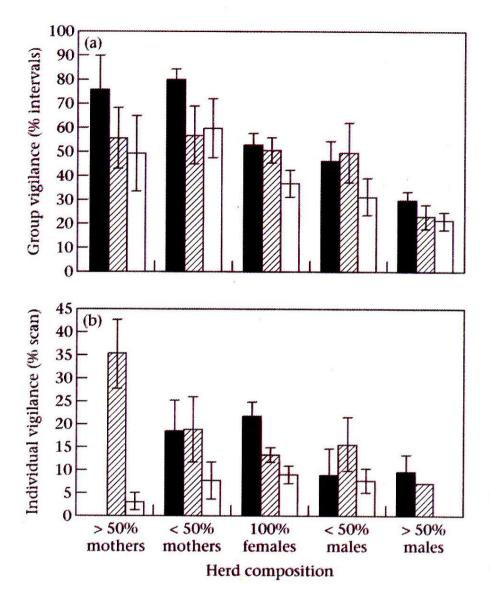


Figure 2 The influence of social status (mother, adult female without calf, yearling, male) and encounter risk (high back; intermediate shaded; low white) on (a) mean \pm SE scan duration (s) and (b) mean \pm SE scan frequency, number of scans (min) of focal individuals (Childres and Lung, 2003).

Females scan their environment longer and with higher frequency because offspring are more predisposed to predation (Childress and Lung, 2003; Kluever *et al.*, 2008). Attacks of predators are the main cause of mortality of large ungulates newborns (Bongi *et al.*, 2008). So vigilance levels are different between females and males (Li and Jiang, 2008). Males and yearlings of red deer (*Cervus elaphus*) need to maximize their fat reserves (Childress and Lung, 2003) so they more forage than scan their environment. But breeding males of impala (*Aepyceros melampus*) are more vigilant because they monitor their rivals and look for possible mates (Li *et al.*, 2009). When youngs grew up their mothers are often less vigilant than with newborns (Kluever *et al.*, 2008).

Z. Li, Z. Jiang and G. Beauchamp

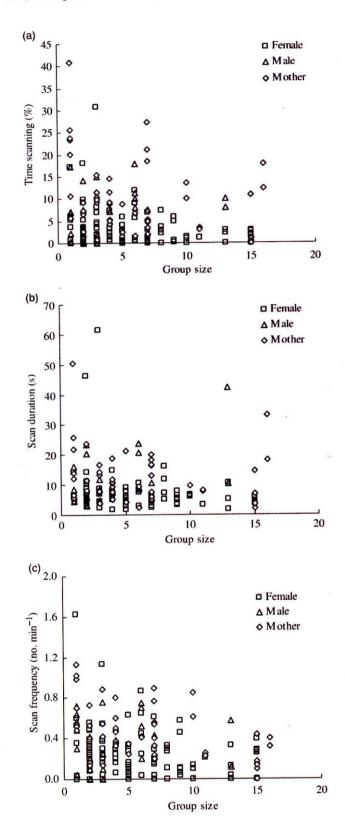


Figure 3 Time spent scanning (a), average scan duration (b) and scan frequency (c) as a function of group size and sex in Przewalski's gazelle *Procapra przewalski* (square: female; triangles: male; diamonds: mother) (Li *et al.*, 2009).

1.5 Age

Other factor which has influence to predation is age of individuals. Predator usually chooses prey which is more vulnerable and easier to catch (Mattisson *et al.*, 2014). This behaviour can save energy and it causes higher probability of catching prey. It follows that young and old animals are generally more exposed to predation (Fig. 4) (Husseman *et al.*, 2003; Mattisson *et al.*, 2014). So zebra show low survival rate of young animals because it is hunted by lions (Owen-Smith and Mason, 2005). But low age is not always the only reason for easier success (Lingle *et al.*, 2008). Choosing of special age classes could have strong impact to prey population. So lynxes (*Lynx lynx*) hunt reindeer calves mainly in summer when they are small and highly vulnerable (Mattisson *et al.*, 2014).

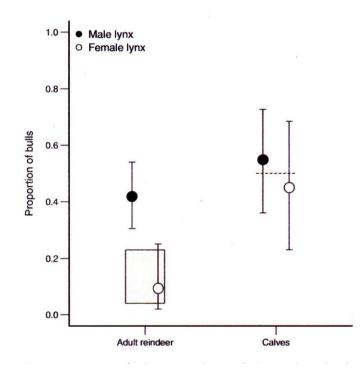


Figure 4 Proportion of bulls among reindeer killed by lynx Lynx lynx in northern Scandinavia in 2006-2011 separated by male and female lynx and the age of reindeer. The grey polygon represents the range of reported bull proportions (adults only) in winter herd among relevant reindeer districts, the striped line shows the expected proportion of males among newborn calves, and error bars are Clopper-Pearson 95% confidence intervals (CIs). A lower CI above the reported range implies selection for bulls/male calves by the lynx (Mattison *et al.*, 2014).

1.6 Prey-predator interactions

The result of predation is not just killing a prey (Fig. 5) (Muhly *et al.*, 2010). Catching a prey is definite but it has not so strong impact to distribution and abundance. The most important impact to system has indirect effects of predator behaviour (Lima, 1998; Creel and Christianson, 2008;

Kluever et al., 2008; Vijayan et al., 2012).

Animals which are hungry more often use more risky habitat. Because foraging animals use more energetically profitable places and they accept high predation risk. Predator occur places which are nutrient richer (Lima, 1998). And their prey often needs to increase their energetic intake. On the other hand indirect predation brings huge influence on population of their prey. Animals need to decrease predation risk so they choose worse pastures. It has influence on their fitness – high level of vigilance causes that animals have not so much time to other activities. Animals can low their own predation rate by another prey. Because alternative prey is more vulnerable and it is easier to catch it for predator (Vijayan *et al.*, 2012). So alternative prey can partially replace preferable prey (Pepin and Shears, 1995). Impact to animals which are usually hunted is that they decrease their vigilance rate (Vijayan *et al.*, 2012). It means original prey expects that predator does not attack it and predator will choose the other prey. Alternative prey could be for predator better than original.

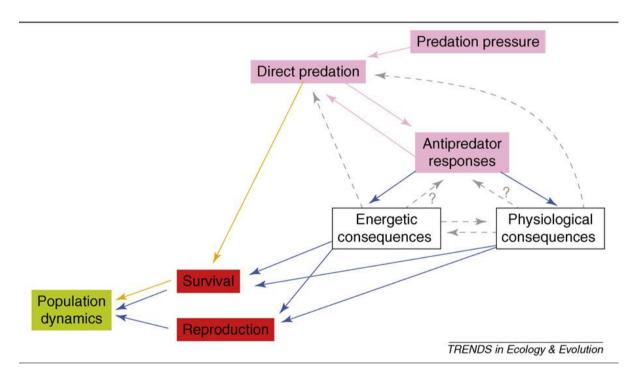


Figure 5 Pathways by which predation can affect the population dynamic of prey: the restricted view that predation operates only through direct offtake is illustrated by two orange arrows linking predation rates to prey dynamics by way of survival; this is only the tip of the iceberg. Pink boxes and arrows illustrated that direct predation rates are not simply an external ecological force imposed on prey by predators, but are determined jointly by the intensity of predation pressure and the antipredator response of prey to that pressure. This creates a feedback loop between direct predation and antipredator responses. In turn, antipredator responses can have physiological or energetic costs for prey, which could alter prey dynamics via either reproduction or survival. These risk effects are illustrated by blue arrows, with likely feedbacks illustrated by gray arrows (Creel and Christianson, 2008).

1.6.1 The role of the time

The day time plays important role because predators hunt in specific time (McNeil *et al.*, 1995; Howery and DeLiberto, 2004; Penteriani *et al.*, 2013). Activity of nocturnal and crepuscular predators depends on external conditions. Prey wants to reduce risk of predation so it will not be so active when predator is ready to hunt (Penteriani *et al.*, 2013). Giant otter (*Pteronura brasiliensis*) is active mostly early morning and early evening (Leuchtenberger *et al.*, 2014) this relates with activity of its prey. Puma and jaguar hunt their prey to and copy their activity in most of cases (Harmsen *et al.*, 2011). Wild rats improved their antipredator behaviour. Rats have nocturnal activity but their predator foxes also are active in this time. So rats changed their activity patterns to day time and when this predation risk disappeared they change their activity back to nocturnal (Apfelbach *et al.*, 2005). Predators are active differently during the year. Predator pressure varyies during some time period and it is really important fact which may shape prey antipredator behaviour (Lingle *et al.*, 2008).

1.7 Role of original predator

Isolation from all predators is rare in wild (Blumstein and Daniel, 2002). It could be on islands where predators are extinct or extirpated or never been there. E.g. predator does not exist for caribou (Rangifer tarandus) on Cost and Southampton Island (Ouellet et al., 1996). In general, valid hypothesis "ghost of predators past" for animals without predators with lower possibility of predation. It means that animals have still antipredator behaviour even though predator does not exist (Blumstein and Daniel, 2002; Blumstein, 2006). Because of these animals were intensively preved in the past. Antipredator behaviour can be maintained during time when there is no risk of predation (Blumstein and Daniel, 2002). Preyed animals can distinguish predators really good. But they have to know danger. It means that higher threat represent native predators. So reaction on historic predator is strong. Many authors wrote about this fact (Apfelbach et al., 2005; Parson et al., 2007; Christensen and Rundgren, 2008; Navarro-Castilla and Barja, 2014). Antipredator behaviour is well developed against most dangerous predator which is often original predator (Mäkeläinen et al., 2014). Parson et al., 2007 found that reaction to natural predator was stronger in kangaroos. They used urine of coyote which is not occurred in Australia and it is unknown for kangaroos so reaction on coyote urine was curiosity. They approached to it. But response to dingo's urine was fright and flight. Kangaroos lived together with dingoes for a long time and the memory of predation was still strong. Similar reaction had white-tailed deer (Odocoileus virginianus dakotensis). Their vigilant behaviour was higher to gray wolf, mountain lion, and coyote faeces than to Bengal tiger. The first three carnivores are native predators for white-tailed deer (Swanson et al., 2002). Native animals often do not cope with alien predator. Such prey is

more vulnerable because it has not quick and good reactions to novel threat (Carthey and Banks, 2012).

1.8 Domestication and its influence on antipredator behaviour

1.8.1 Reduction of antipredator behaviour

Antipredator behaviour can be changed or lost too. It could be caused by many factors. When animals are not exposed to predator they can respond to changing their behaviour. It is matter mainly of islands where animals often lost or have not predator. But antipredator behaviour can persist for many thousands of years without presence of predator. These could be dependent on pleiotropy of this behaviour (Blumstein, 2006).

1.8.2 Antipredator behaviour of domesticated animals

Domestication is more than taming so the process of cattle domestication lasted very long time – about 10,000 years ago (Laporte *et al.*, 2010). It is not presented by two extremes from nature to captivity but it is very slowly and continuous process. Domestic animals are in contact with predator less than free-living animals. Their encounters with predator depend on the type of breeding because many domestic animals never met any predator. It follows that encounter of animals reared in captivity with predator will have worse consequences. E.g. Susceptibility to predation of captive-reared ring-necked pheasants was three times higher than wild-living animals. Artificial selection changes animal behaviour widely. Animals get new types of behaviour and they lost many others. Animals often lost any important ability for living in the wild. E.g. males of domestic turkeys lost ability to copulate and females have to be inseminated (Price, 1999). Animals living in captivity have lower possibility to exhibit their behaviour. And unwanted behaviour is really quick suppressed. So animal is not allowed to breed itself or it is slaughtered.

Domestication plays one of the key roles in cattle. Domestication and artificial selection change cattle behaviour. They became more vulnerable. Livestock have not so quick immediate response to predator like wild ungulates. It could also be due to lack of experiences (Muhly *et al.*, 2010; Laporte *et al.*, 2010). Increasing stress level due to exhibition of antipredator behaviour leads to increase susceptibility to weight loss, get diseases etc. (Laporte *et al.*, 2010). Domestic horses have similar reaction to predator like their wild ancestors. One of the antipredator behaviour is flight. Flight reaction can help them to escape a potential predator. Next behaviour of horses is to react nervously to novel objects. Danger is detected by combination of visual, olfactory and auditory cues (Christensen *et al.*, 2005). But generally

domestic animals show weaker antipredator behaviour reaction than wild animals. On the other hand domesticated animals may learn new antipredator behaviour so livestock know that predator do not come to men close so cattle use safe areas near roads and trails (Muhly *et al.*, 2010). Cattle living on farm in Arizona were attacked by wolves. So these animals never stayed at the same area during one day. Vigilance of these animals increased and as well the level of stress. So animals change their normal behaviour and they started to walk around fences, cows attacked wolves during protection of their calves. Abortion rate of cows was increased after exposition to wolf. Calves started be afraid of cattle dogs because dogs are nearly related to wolves. So these dogs could not control the cattle so long (Howery and DeLiberto, 2004). But cattle still show antipredator behaviour in form of grouping. Get closer may help them to dilute predation risk and not be so vulnerable to predation as an individual because predator may have problem with choosing of its prey (Laporte *et al.*, 2010). Cattle are bred in natural habitats and it is often compete for food with wild ungulates. Bigger groups of livestock may attract predators and this relate with higher predation risk. It is demonstrated by the lions which encounter bigger herd of cattle more frequently (Vijayan *et al.*, 2012).

2 THE AIMS OF THIS THESIS

The main aim of this thesis is determine whether and how cattle on pasture respond to olfactory stimuli. We predict that there could be appear motivation conflict. In our experiment it means that cattle intake the mineral lick even when will be present scent sample what it could be potential danger. But animals in this investigation are long time domesticated. So we expected that domestication and artificial selection could affect reactions of cattle to olfactory stimuli.

Questions

Is there any difference in occurrence of cows between time when the scent was not present and when the control scent was present?

Is there any dependency of weight on frequency and total time of cattle occurrence in licking area?

Is there any difference between two observed pastures?

Hypotheses

H1: We hypothesized that the total time spent in licking area will be longer without scent sample.

H2: We assumed that the frequency of occurrence in area with mineral licks will be higher without scent sample.

3 MATERIALS AND METHODS

3.1 Study area and investigated animals

This study was done on Experimental Station for Fodder Production, Animal Nutrition and Dairy Science – Gut Grunschweige, Eiting, Germany, belonging to Munich Technican University .This farm was located in Freising, Germany. The farm was situated 435-436 meters above sea level, in temperate climate with annual average temperature 7.4°C and annual average precipitation 750 mm.



Figure 6 Cattle on the experimental pasture

Observed cattle was limousine (*Bos primigenius taurus "Limousine*") (Tab. 1). Cattle were bred all year on the pasture (Fig. 6). The farm size was 160 ha, 136.65 ha was grassland and it was divided to several paddocks. This research was done on two of these paddocks. There were 35 individuals (27 individuals in pasture K6 and 8 individuals in pasture K8). In pasture K6 were suckler cows with calves and cows in the second paddock (K8).

Number	K6	Animal	K8	Animal	
1	101544	cow	106059	cow	
2	102018	cow	108209	cow	
3	104302	cow	108225	cow	
4	109246	cow	133359	cow	
5	109548	cow	133361	cow	
6	130824	cow	133448	cow	
7	131424	cow	136417	cow	
8	133371	cow	136655	cow	
9	133456	cow			
10	136579	cow			
11	133416	cow			
12	133372	calf			
13	133376	calf			
14	133389	calf			
15	133399	calf			
16	133421	calf			
17	133422	calf			
18	133430	calf			
19	133431	calf			
20	133432	calf			
21	133441	calf			
22	133461	calf			
23	133463	calf			
24	136386	calf			
25	136421	calf			
26	136459	calf			
27	136601	calf			

Table 1 List of observed animals from pasture K6 and K8

3.2 Data collection

This research was done on two pastures which were situated in the middle of paddocks. It was used pasture K6 (red mark) and K8 (yellow mark), there were bred observed cattle (Fig. 7). These two pastures were really similar.

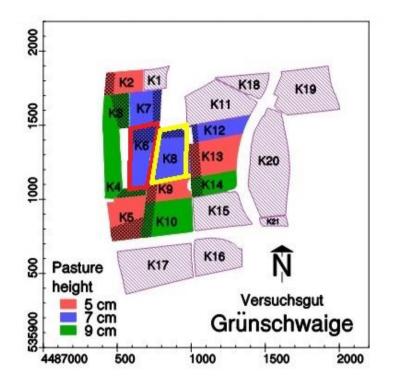


Figure 7 The map of experimental pastures. (K6 - red label and K8 – yellow label were experimental pastures)

Data were collected in July and August 2011 during day and night. All individuals were electronically measured. Cattle had collars with microchips which were included in the place with mineral licks. So when animals came to mineral lick data were recorded in the same time. It means that our data contain total time which individual spent in licking area and also beginning and termination time. There were collected data before and after this research which were used for comparing with our data with predator scent in licking area. Data before this research were similar for both paddock and it was from 28th April 2011 to 28th June 2011. Smells were inserted in period from 29th June to 22th August 2011. Differences began for the last data without odours and there were data picked to 20th October in the pasture K8 and to 2nd November 2011 in K6.

All odours were brought from the Czech Republic. Every scent sample was prepared individual and without possibility of contamination. Cattle could have recognized human smell and it was not considered as contamination. Each scent sample was inserted to the glass jar with fabric, carefully closed. Next the fabric was taken out and it was fixed next to mineral lick. Every scent sample was used just one time. And the glass jar was never used again. The smell was changed with five-day intervals. Stimuli were prepared as a standardized aratex (sterile cotton absorbent squares) (Pinc *et al.*, 2011) sample with three types of odours. The fabric with scent was placed to the construction of mineral lick. The first two scents were odours of two predators: wolf

(*Canis lupus*) which is sympatric predator and African wild dog (*Lycaon pictus*) which is allopatric predator. Eucalyptus oil was used as a neutral stimulus which does not represent natural danger and it was used mainly for control. Always was used just one type of stimulus. During the experiment there were placed different scent samples in our observed pastures. E.g. When the scent sample of African wild dog was present in the first paddock, so in the second pasture was present control sample.



Figure 8 The place where mineral lick on the pasture was placed. The fabric with or without scent was placed on the construction the mineral lick.

3.3 Statistical analyses

The statistical data analyses were done in Software STATISTICA 12 (StatSoft, Tulsa).

In general, frequency of occurrence in licking area, total time spent in licking area and the difference within data after/thereafter and control scent sample were analyzed by general linear model (GLM). Dependent variables were time, frequency, logTime and independent variables were cow number and odour and as random factor cow number. The data did not have normal distribution which was determined by Kolmogorov-Smirnov's test, so data was transform by log10. For dependency of frequency of occurrence in licking area on weight was used linear regression. Comparison of pastures was used also general linear model (GLM) with dependent variables was Time and independent variables pasture and odours.

4 **RESULTS**

We collected a total of 1,889 records of entries to the mineral licking area on pasture K6 1,477 records on pasture K8 during the experiment and time before and after experiment.

4.1 Pasture K6

There were recorded 666 entries records of entries to the licking area during this experiment. The average time spent in licking area was 7:57 minutes (Tab. 2).

Table 2 Frequency of cattle occurrence of cattle in licking area during scent presence in pasture K6

		Time (min.)			
Odour	Frequency (N)	Mean	min	max	SE
CONTROL	402	0:08:13	0:00:14	0:41:42	0:00:21
WOLF	74	0:07:12	0:00:22	0:32:21	0:00:44
LYCAON	84	0:07:40	0:00:44	0:30:22	0:00:42
EUCALYPTUS	106	0:07:39	0:00:20	0:30:47	0:00:44
Total	666	0:07:57	0:00:14	0:41:42	0:00:16

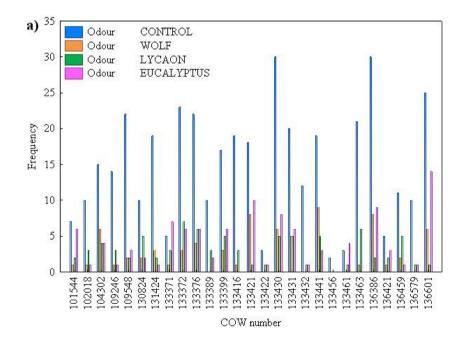
In table 3 there are frequencies of occurrence of each individual in licking area with mean time spent there, standard deviation and standard error of the mean in pasture K6. The most frequent entries to the lick area were 49 times (the cow with ID number 136386) and the least were 2 times (the cow with ID number 133456) but the occurrence in mineral lick was not related with mean time spent there. The individuals with higher number of frequency spent shorter time in licking area. In opposite cow which was in licking area 2 times spent there 22:37 minutes.

Table 3 Frequency of occurrence of each individual in licking area in pasture K6 during experiment

		Time (min.)		
	Frequency		Std.	Std.
Cow number	(N)	Mean	Dev.	Err.
101544	16	0:11:40	0:05:28	0:01:22
102018	15	0:08:06	0:07:20	0:01:54
104302	29	0:11:36	0:06:00	0:01:07
109246	19	0:12:22	0:05:33	0:01:16
109548	29	0:09:48	0:05:35	0:01:02
130824	19	0:11:21	0:07:33	0:01:44
131424	25	0:08:59	0:04:50	0:00:58
133371	16	0:10:49	0:07:51	0:01:58
133372	39	0:08:14	0:08:17	0:01:20

$\begin{array}{cccccccccccccccccccccccccccccccccccc$					
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	133376	38	0:05:27	0:05:35	0:00:54
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	133389	15	0:07:32	0:04:56	0:01:17
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	133399	31	0:03:17	0:02:51	0:00:31
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	133416	23	0:04:08	0:02:34	0:00:32
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	133421	37	0:05:54	0:05:43	0:00:56
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	133422	5	0:04:59	0:04:11	0:01:52
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	133430	49	0:12:05	0:09:49	0:01:24
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	133431	36	0:06:01	0:04:53	0:00:49
13345620:22:370:05:150:03:4313346180:05:380:05:590:02:07133463280:06:410:04:360:00:52136386490:09:100:07:580:01:08136421110:05:430:05:460:01:44136459190:07:180:06:410:01:32136579120:12:590:06:110:01:47	133432	14	0:04:24	0:03:07	0:00:50
13346180:05:380:05:590:02:07133463280:06:410:04:360:00:52136386490:09:100:07:580:01:08136421110:05:430:05:460:01:44136459190:07:180:06:410:01:32136579120:12:590:06:110:01:47	133441	36	0:07:31	0:08:21	0:01:24
133463280:06:410:04:360:00:52136386490:09:100:07:580:01:08136421110:05:430:05:460:01:44136459190:07:180:06:410:01:32136579120:12:590:06:110:01:47	133456	2	0:22:37	0:05:15	0:03:43
136386490:09:100:07:580:01:08136421110:05:430:05:460:01:44136459190:07:180:06:410:01:32136579120:12:590:06:110:01:47	133461	8	0:05:38	0:05:59	0:02:07
136421110:05:430:05:460:01:44136459190:07:180:06:410:01:32136579120:12:590:06:110:01:47	133463	28	0:06:41	0:04:36	0:00:52
136459190:07:180:06:410:01:32136579120:12:590:06:110:01:47	136386	49	0:09:10	0:07:58	0:01:08
136579 12 0:12:59 0:06:11 0:01:47	136421	11	0:05:43	0:05:46	0:01:44
	136459	19	0:07:18	0:06:41	0:01:32
136601 46 0:04:34 0:04:20 0:00:38	136579	12	0:12:59	0:06:11	0:01:47
	136601	46	0:04:34	0:04:20	0:00:38

There were found significant differences in frequency of occurrence in licking area during all scent presence (F=43.5883; p=0.000; Df=3), and also there were significant differences between individuals (F=144.9869; p<0.001; Df=1) (Fig.9). There was the highest occurrence of cattle when there were not sample (called NIC – it means time before and after this experiment). Control sample was more frequented than samples with all three types of scents. So samples with smells of predators and eucalyptus oil had the lowest occurrence (Fig. 10).



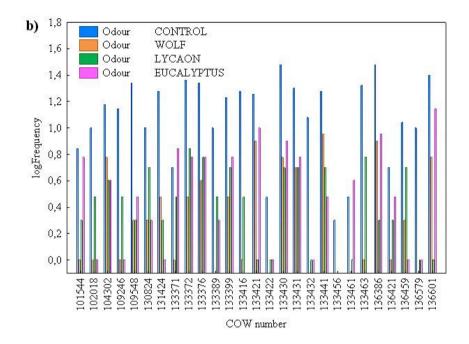


Figure 9 Frequency of occurrence in licking area in pasture K6: a) real frequency data, b) log_{10} transformed data

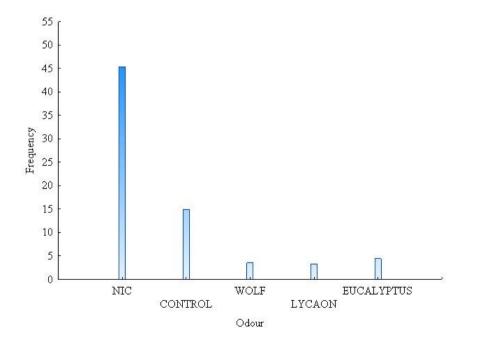


Figure 10 Frequency of entries of cattle to the licking area during, after and thereafter experiment

There was not significant difference in time which was spent in licking area with concrete odour (F=1.163; p=0.3254; Df=3) but there were significant differences between individuals (F=2660.59; p<0.001; Df=1) (Fig. 11).

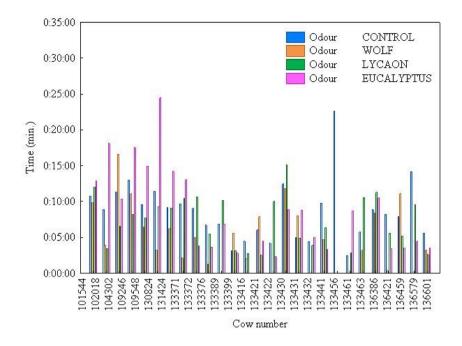
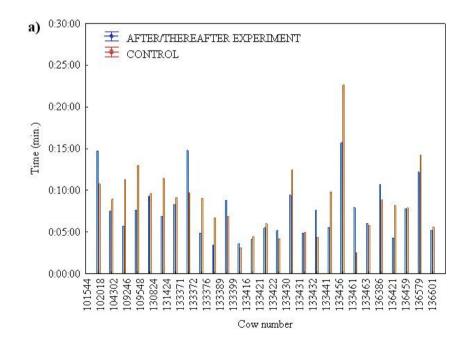


Figure 11 Total time spent in licking area in pasture K6

There were not significant differences in occurrence in licking area between control sample (CONTROL) and mineral lick after and thereafter our experiment (AFTER/THEREAFTER EXPERIMENT) (F=3.055; p=0.08705; Df=1) in pasture K6. There is significant differences in interaction within individuals (F=4995.099; p<0.001; Df=1) in pasture K6 (Fig. 12).



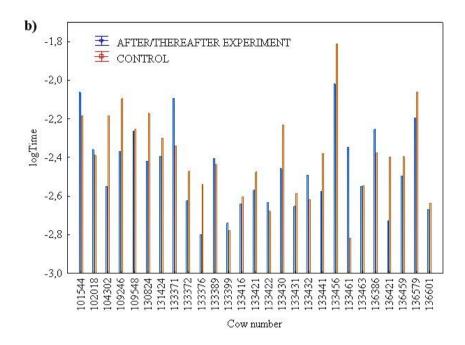
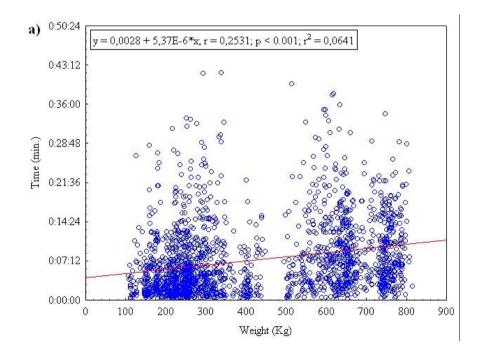


Figure 12 Difference within data after/thereafter experiment and control sample in pasture K6: a) real frequency data, b) \log_{10} transformed data

There are significant differences between total time of occurrence in lick area and weight on pasture K6 (Fig.13): a) real frequency data, b) \log^{10} transformed data, but there is so low number of explanation, so it was not significant result.



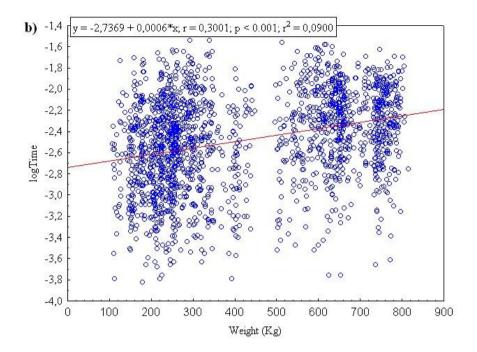


Figure 13 Dependency of weight on frequency and total time of occurrence in licking area in pasture K6: a) real frequency data, b) \log_{10} transformed data

4.2 Pasture K8

There were collected 596 records of entries to the area with mineral lick when scent samples were presented on pasture. The mean time which spent in licking area was quite similar (6:27 minutes) as mean time in pasture K6 (Tab. 4).

Table 4 Frequency of cattle occurrence	in licking area	during scent preser	nce in pasture K8
	0	0	I I I I I I I I I I I I I I I I I I I

		Time (min.)			
Odour	Frequency (N)	Mean	min	max	SE
CONTROL	366	0:06:10	0:04:00	0:35:45	0:00.18
LYCAON	15	0:04:17	0:00:18	0:08:13	0:00.40
EUCALYPTUS	131	0:06:59	0:00:16	0:27:21	0:00:32
WOLF	84	0:07:18	0:00:00	0:32:49	0:00:43
Total	596	0:06:27	0:04:00	0:35:45	0:00:15

The frequency of entries to the licking area is not dependent on scent samples on pasture K8. There were not find any significant differences within types of scent samples. The most frequent was a case with control scent sample there were 366 records of entries to the mineral lick (Tab. 4), but it was lower than number of entries before or/and after experiment.

There were not differences between types of scent samples (F=1.5116; p=0.22145; Df=3), but there were significant differences within individuals (F=865.21; p<0.001; Df=1) (Fig. 14).

And also there were significant differences between after/thereafter and control data on pasture

K8. Cattle spent significantly more time in mineral lick before and after our experiment (Fig. 14).

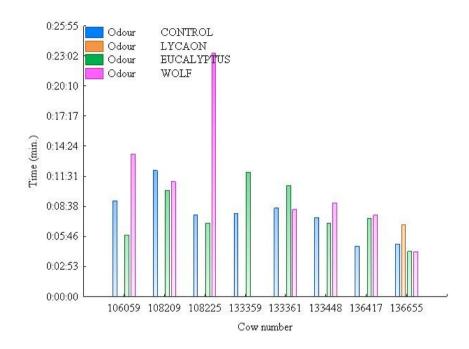
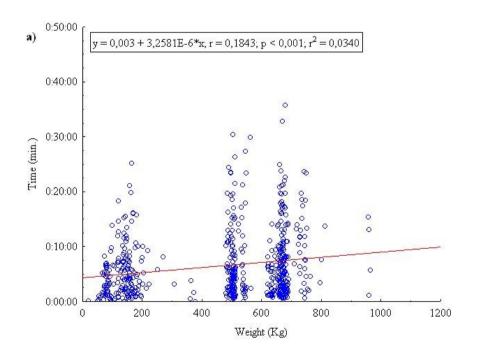


Figure 14 Total time spent in licking area on pasture K8

In case of dependency of weight on occurrence in licking area during scent present there were significant differences on K8 (Fig.15).



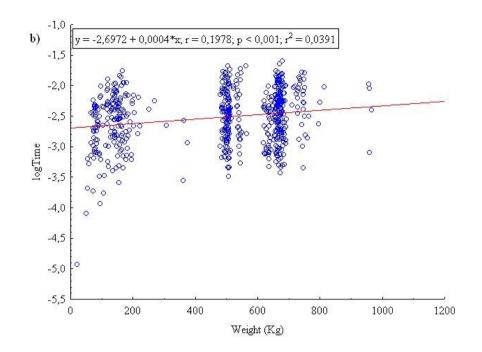


Figure 15 Dependency of weight on frequency and total time of occurrence in licking area in pasture K8: a) real frequency data, b) \log_{10} transformed data

4.3 Difference within pastures K6 and K8

There are significant differences within pastures in mean time spent in licking area (F=4.31; p=0.0382; Df=1) (Fig. 17). The animals spent less time (mean time) on pasture K8 (Tab. 5). But there were not differences between scent samples (F=0.36; p=0.7796; Df=3).

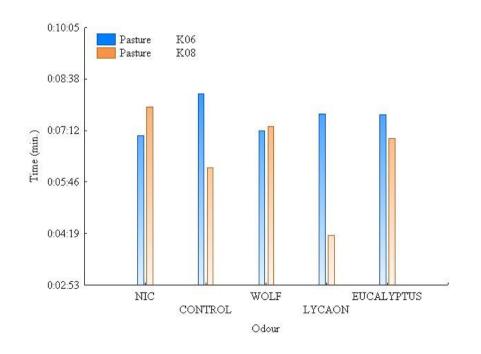


Figure 16 Total time spent in licking areas on pastures K6 and K8

Odour	Pasture	Frequency	Mean Time
CONTROL	K6	402	0:08:13
CONTROL	K8	366	0:06:10
WOLF	K6	74	0:07:12
WOLF	K8	84	0:07:18
LYCAON	K6	84	0:07:40
LYCAON	K8	15	0:04:17
EUCALYPTUS	K6	106	0:07:39
EUCALYPTUS	K8	131	0:06:59
	K6		0:07:57
	K8		0:06:27

Table 5 Frequency and mean time of entries to the mineral lick according type of odours

5 DISCUSSION

Each animal should be avoided its predator and reaction force should correspond to possible danger. Such as wild lemurs (Microcebus murinus and M. ravelobensis) reacted immediately by evading to olfactory stimuli of their native predator fosa (*Cryptoprocta ferox*) which they may met. Lemurs coexist with this predator and they reacted to the olfactory stimuli very stronger than to other potential predator scent (Barn Owl, Tyto alba). So authors decided that fosa is more dangerous for lemurs (Kappel et al., 2011) consequently they react stronger to this predator. But antipredatory behaviour should persist in the case than animal has not met its predator for a long time. As Blumstein and Daniel (2002) predicted in hypothesis "ghost of predator past" so it was assumed to be also in this research. Such as tammar wallabies (Macropus eugenii) still show antipredator behaviour in the case that they have not been exposed to predator for long time. Cattle in this investigation showed significant differences within frequency of occurrence in area with mineral lick during experiment with scent samples. The mineral lick was frequently used in time with control and eucalyptus sample were present. These observed animals were a long time in condition without any potential predator. There were not so much differences between eucalyptus oil and sample of predator. There were just distinctions in samples when animals went to samples with scents less than to sample without any scent. It is similar to research of Terlouw et al. (1998) where cattle spent less time by feeding when odours were presented. They wrote about novelty fear in cattle which was described by Boissy and Bouissou (1995). Terlouw et al. (1998) wrote about conflict of motivations. In this case cattle wanted to minimize danger, tried to be in safe but on the other hand they wanted to explore and got lot of information about this potential danger. Odours of blood and urine of conspecifics and dog faeces caused increase of sniffing and stretched locomotion in similar manner. Smell of dog faeces could indicate presence of native predator. Animals have strong olfactory sensitivity when they can recognized specific smell in low concentration. Cattle in Kluever et al. (2009) research showed distinctive reaction to wolf stimuli. Wild ancestor Bos primigenius lived together with this predator in Eurasia. But reaction to wolf may be due to general respond to all canids (as domestic dogs and wolves) and stalking predator may incite more fear in prey than ambush predator as a mountain lion to which cattle reacted inadequately.

Animals may learn antipredator behaviour as Swanson *et al.* (2002) wrote about young fawns which reacted nervously to feaces of predators. They have never met any predator nevertheless they showed strong antipredator behaviour to their native predator which still lived with them. So authors supposed that it is innate behaviour. Similar research did Parson *et al.* (2007) but he used nonnative predator. Kangaroos reacted strongly to coyote's urine in the case that they have

never met this predator. They called it leitmotif effect when animals may react to unknown predator substantially. In our research animals significantly used mineral lick when there was not present any scent sample. It may be caused by reaction to this smell as an avoidance area with unknown olfaction because there were not so big differences between smell of native predator (wolf), non native predator (African wild dog) and eucalyptus oil. The control sample was more frequently visited than others samples. And cattle visited the area with mineral lick significantly more when there were not samples.

Difference in occurrence when there were control sample and nothing may be depends on vision stimulus. Because vision and audition is usually used as the first sense to recognition of predator (Christensen *et al.*, 2005; Sugnaseelan *et al.*, 2013) so cattle may react to unknown thing (means control sample) in the licking area in the case that there were not smell of predators. Visual stimuli relates with immediate flight reaction (Christensen *et al.*, 2005) so cattle in our research could be careful and they wanted to approach to fabric which was visibly fixed in area in mineral lick construction. The novel object may cause strong reaction of animals and after some time individuals got accustom to the novelty and they may react more calmly (Górecka *et al.*, 2007). Cattle in our research reacted similarly because frequency of cattle occurrence in licking area without any sample was much higher then cattle occurrence with control sample. So the fabric could animals really affect.

There was significant difference between pastures in mean time which cattle spent in licking area. This could be due to different age of animals. On the pasture K8 were adult animals and on pasture K6 were cows and calves. So they could have different need of minerals. But dietetic and nutritional research was not included to this work.

On the other hand lack of response to alopatric predator predator may result more harm. Because unknown predator may has stronger impact to population than native. This predator makes animals more vulnerable and may critically decline its population (Salo *et al.*, 2007). Cattle in this research did not react differently to wolf and African wild dog stimuli. It could be caused by long time without predation. This is a case when animals live in peaceful environment without predator and they do not expect any danger. Other could be long-term breeding and domestication which could make animals more phlegmatic so reactions to predator (native and alopatric predator) are reduced.

Elmeros *et al.* (2011) found similar results as in our experiment that ungulates (red deer *Cervus elaphus*, and roe deer *Capreolus capreolus*) accepted very quickly the scent of wolf. This is

native predator for them and animals often react strongly to this type of predator. But these ungulates did not react significantly and they could get accustom to this smell. They reacted more cautiously but they were not discouraged of area with scent of wolf. This is unexpected because predation is driven by evolution and antipredator behaviour should be instinctive. But response to native predator may not be so strong always. Low reaction of ungulates to odours of coexistence predator may be caused by many factors such as low food availability or weather. Their research was conducted by winter when high risk is expected. We did not find any differences in time which cattle spent in area with mineral lick when odours were presented. But in this research it may be caused by other factors such as breeding, domestication or time which animals spent without encounters with predators. Next reason may be motivation conflict when animal have to choose between feeding and possible predation risk which was presented by samples with predator's smells. Because animals spent lot of their energy by choosing good pasture and there were low predation risk (Kluever et al., 2009) they may risk to entry to the licking area with scent sample assuming possible predation. Christensen et al. (2005) mentioned low reaction to olfactory stimuli as a tactic when smells is slowly brought by air so the immediate reaction of animals would be unnecessary loss of energy.

We tested if weight of animals may affect the reactions to odours. In this case we used weight as indicator of age because there were only suckler cows and calves, so it was very easy to determine what is what according weight. Our assumption of different reactions young and adult animals was not confirmed because calves reacted similar to adult individuals. Usually young animals react more inadequately than adults because lack of experiences with predator and they are more susceptible (Lingle *et al.*, 2005; Cornelia and Temple, 2013; Lashley *et al.*, 2014). But cattle do not need effective antipredator behaviour because they are breed in farms where encounters with predator are minimal or not. Antipredator behaviour could be lost due to artificial selection when animals stay more taming and less aggressive. Exposure to predator may increase stress and it may have impact to fitness – animals are more difficult to reproduce. The productivity of cattle depends on their personality. So domestic animals are breed for calm and fearlessness which increase milk and meat yield (Müller and von Keyserlingk, 2006; Laporte *et al.*, 2010).

6 CONCLUSION

Domestication and separation of animals from predators play important role in antipredator behaviour of ungulates. So reactions of cattle to olfactory stimuli were not so strong. And differences in type of scent sample proved. On the other hand these results are not so surprising because cattle are bred for yield and farmers try to maximize it. If calm temperament may help to animals to increase yield so we can not be surprised that animals did not react so much distinctly to predator odours. If cattle would react to every smell strongly they would be in stress for long time and the yield would be decreased. Also there could be low reactions to predator's smell from other reason as odour of canids species. Because these cattle met domestic dogs often so they were not afraid of them and smell of wild canids is similar to smell of domestic dogs. So for future research would be interesting compare odours of two different predators because animals react differently to smell of stalking predator (dog, wolf) and ambush predator (e.g. lynx). And for additional research will be engaging to find out if reactions to olfactory stimuli are dependent on sex or/and age. These are significant difference in wild living animals because distinctions in antipredator behaviour have impacts to survival.

7 **REFERENCIES**

Abrahams MV, Dill LM. 1989. A determination of the energetic equivalence of the risk of predation. Ecology 70(4): 999-1007.

Ache BW, Young JM. 2005. Olfaction: Diverse species, conserved principles. Neuron 48: 417-430.

Alvarez F. 1993. Alertness signalling in two rail species. Animal Behaviour 46: 1229-1231.

Apfelbach R, Blanchard CD, Blanchard RJ, Hayes RA, McGregor IS. 2005. The effect of predator odors in mammalian prey species: A review of field and laboratory studies. Neuroscience and Biobehavioral Reviews 29: 1123-1144.

Bailey DW, Gross JE, Laca AE, Rittenhouse LR, Coughenour MB, Swift DM, Sims PL. 1996. Mechanisms that result in large herbivore grazing distribution patterns. Journal of Range Management 49(5): 386-400.

Belovsky GE. 1986. Generalist herbivore foraging and its role in competitive interaction. American Zoologist 26: 51-69.

Blumstain DT, Daniel JC. 2002. Isolation from mammalian predators differentially affects two congeners. Behavioral Ecology 13 (5): 657 663.

Blumstein DT. 2006. The multipredator hypothesis and the evolutionary persistence of antipredator behavior. Ethology 112: 209-217.

Boissy A, Bouissou MF. 1995. Assessment of individual differences in behavioural reactions of heifers exposed to various fear-eliciting situations. Applied Animal Behaviour Science 46: 17-31.

Bongi P, Ciuti S, Grignolio S, Del Frate M, Simi S, Gandelli D, Apollonio M. 2008. Anti-predator behaviour space use and habitat selection in female roe deer during the fawning season in a wolf area. Journal of Zoology 276 (3): 242-251.

Brennan PA, Kendrick KM. 2006. Mammalian social odours: attraction and individual recognition. Philosophical Transactions of Royal Society B 361: 2061-2078.

Briefer E, McElligott AG. 2011. Mutual mother-offspring vocal recognition in an ungulate hider species (*Capra hircus*). Animal Cognition 14: 585-598.

Candolin U. 1997. Predation risk affects courtship and attractiveness of competing threespine stickleback males. Behavioural Socio-biology 41: 81-87.

Caro TM. 1986. The functions of stotting in Thomson's gazelles: some tests of the predictions. Animal Behaviour 34(3): 663-684.

Caro TM, Lombardo L, Goldizen AW, Kelly M. 1995. Tail-flagging and other antipredator signals in white-tailed deer: new data and synthesis. Behavioral Ecology 6(4): 442-450.

Caro TM, Graham CM, Stoner CJ, Vargas JK. 2004. Adaptive significance of antipredator behaviour in artiodactyls. Animal Behaviour 67: 205-228.

Carthey AJR, Banks PB. 2012. When does an alien become a native species? A vulnerable native mammal recognizes and responds to its long-term alien predator. PLoS ONE 7(2): e31804.

Childress M, Lung MA. 2003. Predation risk, gender and group size effect: does elk vigilance depend upon the behaviour of conspecifics? Animal Behaviour 66: 389-398.

Christensen JW, Keeling LJ, Nielsen BL. 2005. Responses of horses to novel visual, olfactory and auditory stimuli. Applied Animal Behaviour Science 93: 53-65.

Christensen JW, Rundgren M. 2008. Predator odour *per se* does not frighten domestic horses. Applied Animal Behaviour Science 112: 136-145.

Ciuti S, Pipia A, Ghiandai F, Grignolio S, Apollonio M. 2008. The key role of lamb presence in affecting flight response in Sardinian mouflon (*Ovis orientalis musimon*). Behavioural Processes 77: 408-412.

Corlatti L, Bassano B, Valencak TG, Lovari S. 2013. Foraging strategies associated with alternative reproductive tactics in a large mammal. Journal of Zoology 291: 111-118.

Cornelia F, Temple G. 2013. Loss of anti-predator behaviors in cattle and the increased predation losses by wolves in the Northern Rocky Mountains. Open Journal of Animal Sciences 3(3): 248-253.

Coster-Longman C, Landi M, Turillazza S. 2001. The role of passive defense (selfish herd and dilution effect) in the gregarious nesting of *Liostenogaster* wasps (*Vespidae*, *Hymenoptera*, *Stenogastrinae*). Journal of Insect Behavior 15 (3): 331-350.

Creel S, Christianson D. 2008. Relationships between direct predation and risk effects. Trends in Ecology and Evolution 23 (4): 194-201.

Daleszczyk K. 2004, Mother-calf relationships and maternal investment in European bison *Bison bonasus*. Acta Theriologica 49(4): 555-566.

Devereux CL, Fernández-Juricic E, Krebs JR, Wittingham MJ. 2008. Habitat affects escape behavior and alarm calling in Common Starlings *Sturnus vulgaris*. Ibis 150(1): 191-198.

Devereux CL, Whittingham MJ, Fernández-Juricic E, Vickery JA, Krebs JR. 2006. Predator detection and avoidance by starlings under differing scenarios of predation risk. Behavioral Ecology 17(2): 303-309.

Digweed SM, Fedigan LM, Rendall D. 2005. Variable specificity in the anti-predator vocalizations and behaviour of the white-faced capuchin, *Cebus capucinus*. Behaviour 142(8): 997-1021.

Dumont B, Boissy A. 2000. Grazing behaviour of sheep in a situation of conflict between feeding and social motivations. Behavioral Processes 49: 131-138.

Elmeros M, Winbladh JK, Andersen PN, Madsen AB, Christensen JT. 2011. Effectiveness of odour repellents on red deer (*Cervus elaphus*) and roe deer (*Capreolus*): a field test. Europaean Journal of Wildlife Research 57: 1223-1226.

Evans JP, Kelley JL, Ramnarine IW, Pilastro A. 2002. Female behaviour mediates male courtship under predation risk in the guppy (*Poecilia reticulata*). Behaviour Ecology and Sociobiology 52: 496-502.

Evans DM, Ruxton GD, Ruxton D. 2004. Do false alarm anti-predatory flushes provide a foraging benefit to subdominant species? Biologia, Bratislava 59(5): 675-678.

Fernández-Juricic E, Beauchamp G, Bastain B. 2007. Group-size and distance-toneighbour effects on feeding and vigilance in brown-headed cowbirds. Animal Behaviour 73: 771-778. Fisher DO, Blomberg SP, Owens IPF. 2002. Convergent maternal care strategies in ungulates and macropods. Evolution 56(1): 167-176.

Frommen JG, Hiermes M, Bakker TC. 2009. Disentangling the effects of group size and density on shoaling decisions of three-spined sticklebacks (*Gasterosteus aculeatus*). Behavioral Ecology and Sociobiology 63: 1141-1148.

Gall BG, Mathis A. 2010. Innate predator recognition and the problem of introduced trout. Ethology 116: 47-58.

Gese EM. 1999. Threat of predation: do ungulates behave aggressively towards different members of a coyote pack? Canadian Journal of Zoology 77: 499-503.

Górecka A, Bakuniak M, Chruszczewski MH, Jezierski TA. 2007. A note on the habituation to novelty in horses: handler effect. Animal Science Papers and Reports 25(3): 143-152.

Grovenburg TW, Jenks JA, Jacques CN, Klaver RW, Swanson CC. 2009. Aggressive behavior by free-ranging white-tailed deer. Journal of Mammalogy 90(5): 1218-1223.

Gula R. 2004. Influence of snow cover on wolf *Canis lupus* predation patterns in Bieszczady mountains, Poland. Wildlife Biology 10: 17-23.

Harmsen BJ, Foster RJ, Silver SC, Ostro LET, Doncaster CP. 2011. Jaguar and puma activity patterns in relation to their main prey. Mammalian Biology 76(3): 320-324.

Hebblewhite M, Merrill EH. 2009. Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. Ecology 90(12): 3445-3454.

Hirth DH, McCullough DR. 1977. Evolution of alarm signals in ungulates with special reference to white-tailed deer. The American Naturalist 111(977): 31-42.

Hoogland JL. 1979. The effect of colony size on individual alertness of prairie dogs (*Sciuridae: Cynomys* spp.). Animal Behaviour 27: 394-407.

Howery LD and DeLiberto TJ. 2004. Indirect effects of carnivores on livestock foraging behaviour and production. Sheep and Goat Research Journal 19: 53-57.

Hunter LTB, Skinner JD. 1998. Vigilance behaviour in African ungulates: The role of predation pressure. Beaviour 135: 195-211.

Husseman JS, Murray DL, Power G, Mack C, Wenger CR, Quigley H. 2003. Assessing differential prey selection patterns between two sympatric large carnivores. Oikos 101: 591-601.

Jones KA and Godin JGJ. 2010. Are fast explores slow reactors? Linking personality type and anti-predator behaviour. Proceedings of the Rroyal Society B 277: 625-632.

Kappel F, Hohenbrink S, Radespiel U. 2011. Experimental evidence for olfactory predator recognition in wild mouse lemurs. American Journal of Primatology 73: 928-938.

Kelly CD, Godin JGJ. 2001. Predation risk reduces male-male sexual competition in the Trinidadian guppy (*Poecilia reticulata*). Behavioral Ecology and Sociobiology 51: 95-100.

Kluever BM, Breck SW, Howery LD, Krausman PR, Bergman DL. 2008. Vigilance in cattle: the influence of predation, social interactions, and environmental factors. Rangeland Ecology Management 61: 321-328.

Kluever BM, Howery LD, Breck SW, Bergman DL. 2009. Predator and heterospecific stimuli alter behaviour in cattle. Behavioural Processes 81: 85-91.

Kojola I, Huitu O, Toppinen K, Heikura K, Heikkinen S, Ronkainen S. 2004. Predation on European wild forest reindeer (*Rangifer tarandus*) by wolves (*Canis lupus*) in Finland. Journal of Zoology 263: 229-235.

LaGory KE. 1987. The influence of habitat and group characteristics on the alarm and flight response of white-tailed deer. Animal Behaviour 35(1): 20-25.

Laporte I, Muhly TB, Pitt JA, Alexander M, Musiani M. 2010. Effects of wolves on elk and cattle behaviors: implications for livestock production. PLoS ONE 5(8): e11954.

Lashley MA, Chitwood MC, Biggerstaff MT, Morina DL, Moorman CE, DePerno CS. 2014. White-tailed deer vigilance: The influence of social and environmental factors. PLoS ONE 9(3): e90652.

Leuchtenberger C, Zucco CA, Ribas C, Magnusson W, Mourao G. 2014. Activity patterns of giant otters recorded by telemetry and camera traps. Ethology Ecology and Evolution 26(1): 19-28.

Li Z, Jiang Z. 2008. Group size effect on vigilance: Evidence from Tibetan gazelle in Upper Buha River, Qinghai-Tibet Plateau. Behavioural Processes 78: 25-28.

Li Z, Jiang Z, Beauchamp G. 2009. Vigilance in Przewalski's gazelle: effects of sex, predation risk and group size. Journal of Zoology 277: 302-308.

Li C, Yang X, Ding Y, Zhang L, Fang H, Tang S, Jiang Z. 2011. Do Père David's deer lose memories of their ancestral predators? PLoS ONE 6(8): e53052.

Lima SL. 1995. Back to the basics of anti-predatory vigilance the group size effect. Animal Behaviour 49: 11-20.

Lima SL. 1998. Nonlethal effects in the ecology of predator-prey interactions. Bioscience 48(1): 25-34.

Lima SL and Dill LM. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68: 619-640.

Lima SL, Zollner PA, Bednekoff PA. 1999. Predation, scramble competition, and the vigilance group size effect in dark-eyed juncos (*Junco hyemalis*). Behavioral Ecology and Sociobiology 46: 110-116.

Lingle S, Pellis SM. 2002. Fight or flight? Antipredator behavior and the escalation of coyote encounters with deer. Oecologia 131: 154-164.

Lingle S, Pellis SM, Wilson FW. 2005. Interspecific variation in antipredator behaviour leads to differential vulnerability of mule deer and white-tailed deer fawns early in life. Journal of Animal Ecology 74: 1140-1149.

Lingle S, Feldman AF, Boyce MS, Wilson WF. 2008. Prey behavior, age-dependent vulnerability, and predation rates. The American Naturalist 172(5): 712-725.

Marino A. 2012. Indirect measures of reproductive effort in a resource defence polygynous ungulate: territorial defense by male guanacos. Journal of Ethology 30: 83-91.

Mattisson J, Arntsen GB, Nilsen EB, Loe LE, Linnell JDC, Odden J, Persson J, Andrén H. 2014. Lynx predation on semi-domestic reindeer: do age and sex matter? Journal of Zoology 292: 56-63.

Mäkeläinen S, Trebatická L, Sundell J, Ylönen H. 2014. Different escape tactics of two vole species affect the success of the hunting predator, the least weasel. Behavioral Ecology and Socio-biology 68: 31-40.

McNeil R, Díaz OD, Linero I, Rodriguez JR. 1995. Day- and night-time prey available for waterbirds in tropical lagoon. Canadian Journal of Zoology 73: 869-878.

Messier F. 1994. Ungulate population models with predation: A case study with the north American moose. Ecology 75(2): 478-488.

Moore WG, Marchington L. 1974. Marking behaviour and its social function in whitetailed deer. Geist V, Walther F editors. The behaviour of ungulates and its relation to management. Morges, Switzerland: Unwin Brother Limited, p447-456.

Morgantini LE, Hudson RJ. 1985. Changes in diets of wapiti during a hunting season. Journal of Range Management 38(1): 77-79.

Muhly TB, Alexander M, Boyce MS, Creasey R, Hebblewhite M, Paton D, Pitt JA, Musiani M. 2010. Differential risk effects of wolves on wild versus domestic prey have consequences for conservation. Oikos, 119: 1243-1254.

Müller R, von Keyserlingk MAG. 2006. Consistency of flight speed and its correlation to productivity and to personality in *Bos Taurus* beef cattle. Applied Animal Behaviour Science 99: 193-204.

Müller-Schwarze D. 1974. Social function of various scent glands in certain ungulates and the problems encountered in experimental studies of scent communication. Geist V, Walther F editors. The behaviour of ungulates and its relation to management. Morges, Switzerland: Unwin Brother Limited, p107-113.

Murray DL, Roth JD, Wirsing AJ. 2004. Predation risk avoidance by terrestrial amphibians: the role of prey experience and vulnerability to native and exotic predators. Ethology 110: 635-647.

Navarro-Castilla Á, Barja I. 2014. Antipredatory response and food intake in wood mice (*Apodemus sylvaticus*) under simulated predation risk by resident and novel carnivorous predator. Ethology 120: 90-98.

Nelson ME, Mec LD. 1986. Relationship between snow depth and gray wolf predation on white-tailed deer. The Journal of Wildlife Management 50(3): 471-474.

Niemalä PT, DiRienzo N, Hendrick AV. 2012. Predation-induced changes in the boldness of naïve field crickets, *Gryllus integer*, depends on behavioural type. Animal Behaviour

84: (129-135).

Ouellet JP, Heard DC, Mulders R. 1996. Population ecology of caribou population without predator: Southampton and Cost Island herds. Rangifer 9: 17-26.

Owen-Smith N, Mason DR. 2005. Comparative changes in adult vs. juvenile survival affecting population trends of African ungulates. Journal of Animal Ecology 74: 762-773.

Panzacchi M, Herfindal I, Linell JDC, Odden M, Odden J, Andersen R. 2010. Trade-offs between maternal foraging and fawn predation risk in an income breeder. Behavioral Ecology and Sociobiology 64: 1267-1278.

Parsons MH, Lamont BB, Kovacs BR, Davies SJJF. 2007. Effect of novel and historic predator urines on semi-wild western grey kangaroos. The Journal of Wildlife Management 71(4): 1225-1228.

Penteriani V, Kuparinen A, del Mar Delgado M, Palomares F, López-Bao JV, Fedriani JM, Calzada J, Moreno S, Villafuerte R, Campioni L, Lourenco R. 2013. Response of a top and meso predator and their prey to moon phases. Oecologia 173: 753-766.

Pepin P, Shears TH. 1995. Influence of body size and alternate prey abundance on the risk of predator to fish larvae. Marine Ecology Progress Series 128: 279-285.

Pinc L, Bartoš L, Reslová A, Kotrba R. 2011. Dogs discriminate identical twins. PLoS ONE 6(6): e20704.

Price EO. 1999. Behavioral development in animals undergoing domestication. Applied Animal Behaviour Science 65: 245-271.

Rails K. 1974. Scent marking in captive Maxwell's duikers. Geist V, Walther F editors. The behaviour of ungulates and its relation to management. Morges, Switzerland: Unwin Brother Limited, p114-123.

Reboreda JC, Fernandez GJ. 1997. Sexual, seasonal and group size differences in the allocation of time between vigilance and feeding in the greater rhea, *Rhea americana*. Ethology 103: 198-297.

Roberts G. 1996. Why individual vigilance declines as group size increases. Animal Behaviour 51: 1077-1086.

Robinette RL, Ha JC. 2001. Social and ecological factors influencing vigilance by northwestern crows, *Corvus caurinus*. Animal Behaviour 62: 447-452.

Salo P, Korpimäki E, Banks PB, Nordström M, Dickman CR. 2007. Alien predators are more dangerous than native predators to prey populations. Proceedings of the Royal Society B 274: 1237-1243.

Schel AM, Tranquilli S, Zuberbühler K. 2009. The alarm call system of two species of black-and-white colobus monkey (*Colobus polykomos* and *Colobus guareza*). Journal of Comparative Psychology 123(2): 136-150.

Stankowich T. 2008. Tail-flicking, tail-flagging and tail position in ungulates with special reference to black-tailed deer. Ethology 114: 875-885.

Stevens M, Yule DH, Ruxton GD. 2008. Dazzle coloration and prey movement. Proceedings of the royal society B 275: 2639-2643.

Sugnaseelan S, Prescott NB, Broom DM, Wathes CM, Phillips CJC. 2013. Visual discrimination learning and spatial acuity in sheep. Applied Animal Behaviour Science 147: 104-111.

Swanson CC, Kassube CM, Jenks JA. 2002. White-tailed deer behavioral response to predator feces. Proceeding of the South Dakota Academy of Science 81: 143- 146.

Terlouw EMC, Boissy A, Blinet P. 1998. Behavioural responses of cattle to the odours of blood and urine from conspecifics and to the odour of faeces from carnivores. Applied Animal Behaviour Science 57: 9-21.

Thaker M, Vanak AT, Owen CR, Ogden MB, Slotow R. 2010. Group dynamics of zebra and wildebeest in a woodland savanna: Effects of predation risk and habitat density. PLoS ONE 5(9): e12758.

Torriani MV, Vannoni E, McElligott AG. 2006. Mother-young recognition in an ungulate hider species: A Unidirectional Process. The American naturalist 168(3): 412-420.

Turner GF, Pitcher TJ. 1986. Attack abatement: A model for group protection by combined avoidance and dilution. The American Naturalist 128(2): 228-240.

Vijayan S, Morris DW, McLaren BE. 2012. Prey habitat selection under shared

predation: Tradeoffs between risk and competition? Oikos 121: 783-789.

Walters JR. 1990. Anti-predatory behavior of lapwings: field evidence of discriminative abilities. The Wilson Bulletin 102(1): 49-70.

Xu F, Ma M, Wu Y. 2010. Group size and sex effects on vigilance: evidence from Asiatic ibex, *Capra sibirica* in Tianshan Mountains, China. Folia Zoologica 59(4): 308-312.

Xu F, Ma M, Yang W, Blank D, Ding P, Zhang T. 2013. Group size effect on vigilance and daytime activity budgets of *Equus kiang* (*Equidae*, *Perissodactyla*) in Arjinshan National Nature Reserve, Xinjiang, China. Folia Zoologica 62(1): 76-81.