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**Acoustic aspects of antipredator behaviour in Blue wildebeest
(*Connochaetes taurinus*)**

Diploma thesis

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Affirmation

I declare hereby that this diploma thesis on the theme: Acoustic aspects of antipredator behaviour in Blue wildebeest (*Connochaetes taurinus*) was elaborated independently and is based only on my own knowledge, consultations with my supervisor and literary resources cited in attached bibliography.

In Prague 18th April 2014

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Abstract

Acoustic aspects of antipredator behaviour in Blue wildebeest (*Connochaetes taurinus*)

Many animals are able to distinguish predator calls and alarm calls emitted by other species. However, a little attention was paid to this ability in African ungulates.

I performed playback experiments in Kruger National Park to examine whether blue wildebeests (*Connochaetes taurinus*) recognize loud calls of predators and alarm calls of other species. I used lion's (*Panthera leo*) and spotted hyena's (*Crocuta crocuta*) loud calls and greater kudu's (*Tragelaphus strepsiceros*) and helmeted guineafowl's (*Numida meleagris*) alarm calls.

I found out that wildebeests distinguish all treatment calls used (lion, hyena, kudu, guineafowl) from control calls. The ability to recognize the potential danger could be crucial to ensure the survival of wildebeests. The most common response of tested individuals was turning their head or look toward the source of sound. I did not discover significant difference in responses to different treatment stimuli (lion, hyena calls and kudu, guineafowl alarm calls); this could suggest similar antipredator strategy in wildebeests. Furthermore, based on my results, responses were influenced by daytime, group size, habitat and presence of other species. Wildebeests responded with greater intensity in the early morning and late afternoon, with the growing herd size the latency of responses increased, solitary individuals responded more intense than individuals in herds, reactions were shorter in the bush and wildebeests reacted faster in the presence of other species.

Cognitive abilities of ungulates during predation interactions represent a broad range of questions to resolve. Beside this, the understanding of prey-predator interactions could be crucial for starting diverse re-introduction programmes and acoustic interactions may play an essential role in difficult conservation effort.

Key words:

predation, vigilance, alarms call, heterospecific signals

Anotace

Akustické aspekty antipredačního chování pakoně žíhaného (*Connochaetes taurinus*)

Mnoho zvířat má schopnost rozpoznat volání predátorů a varovná volání jiných živočišných druhů. Zatím však bylo velmi málo pozornosti věnováno této schopnosti u afrických kopytníků.

Pomocí playbackových experimentů v Krügerově národním parku jsem testovala schopnost pakoně žíhaného (*Connochaetes taurinus*), zda rozeznává volání predátorů a alarmy jiných zvířat. Použila jsem volání lva (*Panthera leo*) a hyeny skvrnitě (*Crocuta crocuta*) a varovné volání kudu velkého (*Tragelaphus strepsiceros*) a perličky kropenaté (*Numida meleagris*).

Zjistila jsem, že pakoně rozlišují všechny použité hlasy (lva, hyeny, kudu, perličky) od kontrolních zvuků. Schopnost rozeznat hrozící nebezpečí může být zásadní pro zajištění přežití pakoňů. Nejčastější reakcí zkoumaných jedinců bylo otočení hlavy nebo pohled směrem ke zdroji zvuku. Nejistila jsem signifikantní rozdíly v reakcích na použité hlasy, což by mohlo naznačovat podobnou antipredační strategii pakoňů.

Podle mých výsledků byly reakce ovlivněny denní dobou, velikostí skupiny, prostředím a přítomností jiných druhů. Pakoně reagovali s větší intenzitou v časných ranních a pozdních odpoledních hodinách, s rostoucí velikostí stáda latence reakcí rostla, jednotlivci reagovali intenzivněji než jedinci ve stádech, reakce byly kratší v buši a pakoně reagovali rychleji v přítomnosti jiných druhů.

Kognitivní schopnosti kopytníků během interakcí s predátory přináší mnoho otázek, na které doposud neznáme odpovědi.

Mimo to, porozumění interakcím mezi kořistí a predátorem je klíčové pro začátek různých reintrodukčních programů a akustické interakce mohou hrát zásadní roli při komplikovaném procesu ochrany přírody.

Klíčová slova:

predace, ostražitost, varovné volání, heterospecifické signály

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1 Introduction

Animal communication is characterized by great diversity, animals communicate to protect their territory, to find a partner for mating, to get food, to avoid predators etc. (Dugatkin, 2003). Acoustic signals play a crucial part in the prey-predator interactions.

Predation belongs among the main forces which form the animal behaviour (Tuttle and Ryan, 1981) and several species evolved various antipredation behaviour. For example early detection of predator significantly lowers the predation risk (Lima and Dill, 1990; Katz and Dill, 1998; Stankowich and Blumstein, 2005).

There are two main acoustic sources the prey may rely on for an instant recognition of predators. It can eavesdrop to predator vocalizations or listen to highly advantageous alarm calls of heterospecifics (individuals of different species) (Randler, 2006). Predators often aggregate and live in the neighbourhood of their prey. Although they usually do not vocalize during the hunt (Estes, 1991) the prey has a possibility to notice them during other activities like signalling territory occupancy, contact with group members etc. (Grinnell and McComb, 1995).

Many studies demonstrated that several species of mammals and birds respond adequately to predator vocalizations by increased vigilance (reviewed by Blumstein et al., 2008; Hettner et al., 2014).

Communication primarily evolved in order to communicate with the conspecifics (e.g. individuals of the same species); nevertheless the signals transferred between conspecifics can be also caught by the heterospecifics. Heterospecific communication is especially favourable in prey-predator interactions. The prey can inform other species about predator's occurrence through alarm calls (e.g. Shriner, 1998; Ramakrishnan and Coss, 2000; Fichtel, 2004). Many studies in taxonomically related species (Carrasco and Blumstein, 2012) have pointed out the recognition of interspecies alarm calls. But recognition of interspecies signals occurs also between different classes of vertebrates like birds and mammals (e.g. Zuberbühler, 2000; Flower, 2011), even between birds and reptiles (Vitousek et al., 2007; Ito and Mori, 2010).

Despite the fact that the understanding of alarm and predator calls is intensively studied within animals, African ungulates belong among the least studied groups of animals. Surprisingly regarding the wildebeests, just one study was focused on this common gregarious ungulate species. It was discovered that they distinguish between

baboon's alarms and their contest calls (Kitchen et al., 2010). This finding could indicate that wildebeests might be able to recognize alarm calls of other heterospecifics.

A little attention was paid to interspecies alarm call recognition within African ungulates and birds (Lea et al., 2008). The lack of information in this field inspired me to test whether wildebeests are able to recognize alarm calls of constantly alert sympatric helmeted quineafowl that often join herds of herbivores in Africa.

In spite of widely studied interspecies alarm call recognition, I did not find a study focused on recognition within different species of ungulates. To begin addressing these knowledge gaps I performed field experiments to test whether wildebeests recognize kudus' alarm calls.

In some African ungulates (impalas, kudus, dik-diks) the ability to distinguish loud calls of their natural predators was observed (Blanchard and Fritz, 2007; Coleman et al., 2008; Meer et al., 2012; Favreau et al., 2013). This fact led me to examine if wildebeests poses this ability as well.

2 Literature Review

2.1 Antipredator behaviour

Predators have a strong effect on prey species behaviour, abundance and distribution (Tuttle and Ryan, 1981; Valeix et al., 2009) and predation is a major source of natural selection (Lima and Dill, 1990). Animals count on the risk of predation when deciding how to behave for example considering mating opportunities (Katz and Dill, 1998). In Neotropics frogs selective advantage of loud mating calls is balanced by the increased risk of predation by fringe-lipped bats (*Trachops cirrhosis*) (Tuttle and Ryan, 1981).

Animals are able to detect predator's presence and evaluate predation risk through different sensory channels: visual, electrical, chemical, vibratory, tactile and auditory (Lima and Dill, 1990). In prey-predator interactions acoustic cues bring many advantages. They can be received immediately, are long in range and may pass barriers (Alcock, 1984).

In many species we can find different types of antipredator behaviour. Some species remain motionless or freeze (e.g. steenbok, oribi), hide into the burrow (e.g. common warthog), others start to leap in all directions (e.g. impalas), inspect the predator (e.g. Thomson's gazelles, blesbok), bunch together (e.g. buffalo, common eland), even try to attack the predators (e.g. sable antelope, gemsbok) etc. (Caro et al., 2004).

2.2 Antipredator behaviour of Blue wildebeest

Wildebeests are gregarious large herbivores of African savannah. They are the preferred prey of large predators, especially lions and hyenas. Males weighing 250 kg are within the lions' preferred prey body mass range (Hayward and Kerley, 2005). In the Kruger National Park (KNP), the lions were and continue to be wildebeests' principal predators (Fay and Greeff, 2006) (Fig.1.).



Fig.1. Lion with its preferred prey - wildebeest in KNP (own collection, © Zuzana Panovská).

Wildebeests' typical antipredator defence is foot stamp, bunch together, approach a lion in the alert posture or performance of style-trot. They often trail or follow the predators trying to ward them off and mothers can defend their calves with considerable success (Fig.2.). When a potential predator is identified they utter a loud shrill alarm snort (Estes, 1991). Sinclair (1985) believed that wildebeests escape the predation through formation of extremely large herds, leading to predation saturation.



Fig.2. Herd of wildebeests with calf in KNP (own collection, © Zuzana Panovská).

2.3 Vigilance

If the prey detects the presence of the predator in time it decreases the predation risk (Lima and Dill, 1990; Katz and Dill, 1998; Stankowich and Blumstein, 2005). Vigilance as scanning of the surrounding and searching for predators is major antipredator behaviour (Lima and Dill, 1990). It demands time and energy and it may lead to disrupting of feeding behaviour (Bachman, 1993).

It is widely accepted that the predator detection is the major function of vigilance. However, many ungulates live in social groups where they need to coordinate their movements with the other members and so interactions among individuals are maintained by vision. Furthermore, herbivores find food by eye so reasons for being alert may be more complex than just looking for predators (Hunter and Skinner, 1998).

The relative proportions of vigilance time devoted to antipredator versus social vigilance vary among species, probably due to the differences in species' vulnerabilities to predation and differences in their social behaviours (Favreau et al., 2013).

2.3.1 Factors affecting vigilance

Many factors like presence of the predator, predation pressure, group size, presence of other species, sex, distance to the nearest cover, time of the day, location in the herd, etc. can affect vigilance (Quenette, 1990). Blanchard and Fritz (2007) claim that vigilance has two components: induced vigilance when responding to a stimulus indicating for example predator presence and routine vigilance when the animal is monitoring its surroundings during spare time.

In the site with high predation (where large felids were re-introduced), rate of looking and proportion of time spent looking by impalas and wildebeests was significantly greater than in the site with low predation (Hunter and Skinner, 1998).

In many vertebrates, such as birds and mammals, time spent vigilant decreases as group size increases (e.g. Burger and Gochfeld, 1993; Roberts, 1996). From the presence of conspecifics benefit many animals by reducing their scanning rate for predators while increasing their time for foraging (Childress and Lung, 2003). This group size effect could arise from an increased ability to detect predators - many eyes hypothesis (Powell, 1974) or decreased perception of individual risk - dilution hypothesis (Dehn, 1990). Individuals can also benefit from the early warning of mix-species associations if the information that predator has been detected is transmitted to the others and if all group members are alert to the same predator species (Metcalf, 1984). An additional benefit of mixed species grouping may occur if predators show preference for a particular prey species (Fitzbibbon, 1990). Sinclair (1985) found in the Serengeti that zebras (*Equus burchelli*) can reduce their predation risk by staying close to wildebeests (*Connochaetes taurinus*), the preferred prey of the large carnivores in the area.

It was observed in several studies that females are less vigilant during grazing than males. It was found out for ungulates like: wildebeest, zebra, waterbuck, kob (Burger and Gochfeld, 1994), buffalo (Prins and Iason, 1989) and springbok (Burger et al., 2000). This difference seems to be connected to males watching for competitors and mates as well as watching for predators (Burger et al., 2000). On the other hand for example in elk it was observed that adult males were the least vigilant. They fed the most and were not influenced by an encounter risk or a herd size (Childress and Lung, 2003). In general we can say that females with young are more vigilant than females without young, because

juveniles are exposed to a greater predation risk (Burger and Gochfeld, 1994; Hunter and Skinner, 1998).

Cover, provided by vegetation, can influence behaviour in many ways. The time spent vigilant increases with cover and vegetation height because it decreases the distance from which the predators can be detected and decreases the early warning time (Lagory, 1986). Underwood (1982) found out that ungulates increased their vigilance in thick vegetation compared to sparse cover. The distance to cover may also reflect the distance that the prey must reach to hide from predators, or provide places for predators to hide while stalking those (Burger et al., 2000).

Animals are likely to increase vigilance during the time frames when predators are more likely to hunt. Predator-sensitive hours are for example early morning when natural predation risk peaks because of an overlap of time frames at which both nocturnal (lion and spotted hyena) and diurnal (African wild dog) predators hunt (Meer et al., 2012).

Several studies on African ungulates have demonstrated that animals on the edge of herds spent more time vigilant than individuals in the centre, probably because they were more exposed to an attack (Underwood, 1982; Bednekoff and Ritter, 1994; Burger and Gochfeld, 1994; Hunter and Skinner, 1998).

2.4 Acoustic discrimination of predators

Acoustic signals often play a very important role in anti-predatory behaviour. It is known that predators frequently aggregate and live near their prey. Although they usually do not vocalize during the hunt (Estes, 1991) the prey has a possibility to notice them during other activities. Predators use loud calls for various purposes such as defending their territory (e.g. lions; Ramsauer, 2005), reuniting of pack members, expressing the excitement before hunting (e.g. African wild dog; Estes and Goddard, 1967) and communicating with other group members (e.g. African wild dog, Estes and Goddard, 1967; lions, Mc Comb et al., 1994).

Predator discrimination capabilities may be present from birth (Hettena, 2014), achieved through direct interactions with predation (Chivers and Ferrari, 2013) or may also be learned by observing the behaviours of heterospecifics (Fallow et al., 2013) or conspecifics (Griffin, 2009).

In many mammals like primates, carnivores, marsupials, rodents and bird species it was observed that they respond to predator vocalizations by increased vigilance or escape

(reviewed in Blumstein et al., 2008). Hettena et al. (2014) reviewed predator playback studies (on both vertebrates and invertebrates) based on the type of prey-predator experience: neither evolutionary nor ecological, evolutionary, ecological or both. According to the review most of the studies used predatory stimuli to which prey had both ecological and evolutionary exposure and prey tended to discriminate this sort of predator.

Some playback studies have the potential to explain the mechanism that underlies acoustic predator discrimination. The fact that the prey respond to a novel predator suggests that discrimination may occur by prey using certain acoustic characteristics. Stimuli produced by novel predators may have these characteristics in common with known predators (Hettena et al., 2014).

2.4.1 Recognition of predator calls in ungulates

In mammals, studies were biased toward primates and rodents, however, studies on ungulates, focused on behavioural responses to sound signals of their natural predators, belong to less common ones. In mule deer (*Odocoileus hemionus*) the capability to distinguish among familiar predators such as coyotes (*Canis latrans*) and mountain lions (*Puma concolor*) and locally extinct wolves (*Canis lupus*) was observed. The amount of time spent showing a heightened response to coyote and wolf playbacks was significantly different from the responses to control playback and the response to the mountain lion was not significantly different. It means that mule deer preserved the ability to respond to the extinct wolf and responded stronger to canids than to felids (Hettena et al., 2014). In contrast Li et al. (2011) found out that Père David's deer (*Elaphurus davidianus*) approached and stared toward the calls of the ancestral predator - tiger and potential predator - lion more than to canids calls. They approached tiger roars more, listened to them longer, stags foraged less and it took them more time to come back to their normal behaviour. Père David's deer retain the memories of their ancient predator but also respond to the novel predator lion. Berger et al. (2001) tested the possible susceptibility of European moose (*Alces alces*) to unfamiliar predators and observed that responses to auditory cues were conspicuously less among predator-naïve moose and that vigilance in predator-experienced populations increased with wolf calls. However, in moose the ability to reduce responsiveness to extinct predators returned in single generation (Berger et al., 2007).

2.4.2 Recognition of predator calls in African ungulates

A few studies are focused on testing the impact of predator calls on African ungulates behaviour. Favreau et al. (2013) tested how lion roars effect foraging, vigilance and movement of female impalas. In impalas exposed to lion calls the amount of time vigilant (without chewing) was significantly greater and bite rates decreased compared to pre-playback period and they significantly increased their step rates compared to control stimuli (Favreau et al., 2013). Blanchard and Fritz (2007) found similar results, although they concentrated only on the first vigilant bout of impalas in response to playbacks of lions' calls. They found out that alarmed impalas increased their use of exclusive vigilance compared to non-alarmed individuals. When responding to an external controlled stimulus, impalas raised their head faster, waited for a much longer time before initiating the first chew and chewed less compared to the situation where the observer did not induce vigilance.

Meer et al. (2012) studied the effects of African wild dog calls and faeces distribution on behaviour of kudus and impalas and discovered little effect on their behaviour. Only immediate predator presence resulted in high-quality vigilance by kudu. Environmental variables such as visibility in the habitat and the time of the day seemed to influence primarily their anti-predator behaviour.

To discover the consequences of habituation to human presence Coleman et al. (2008) broadcasted playbacks of side-striped jackal (*Canis adustus*) and non-threatening bird to Gunther's dik-diks (*Madoqua guentheri*) in areas where dik-diks were and were not habituated to humans. Contrary to their expectation, dik-diks did not distinguish among playbacks stimuli farther from human settlements. They reduced vigilance and exhibited a small difference in foraging and nose twitching.

2.4.3 Ability to recognize predator calls in other species

Even in the species like elephants it was observed that predator vocalization had an effect on their behaviour. Elephants reacted similarly carefully to the simulated presence of tiger and leopard by finally moving away but the difference was in instant behaviour. Elephants moved away silently after tiger calls, while they displayed aggressive vocalizations and alert or investigative behaviours to leopard calls (Thuppil and Coss, 2013).

In family groups of African elephants it was observed that sensitivity to threat caused by lion's playbacks increases with matriarch age (McComb et al., 2011).

We can find the acoustic identifying of predators also in water mammals. Harbour seals (*Phoca vitulina*) reacted strongly to calls of mammal-eating killer whales and unfamiliar fish-eating killer whales, but did not respond to the familiar calls of the local fish-eating population (Deecke et al., 2002). Kuker (2010) revealed that sea otters (*Enhydra lutris*) in the Aleutian Islands responded to both control and treatment playbacks of killer whale while the sea otters in British Columbia did not, so it suggests that there is some form of environmental difference between these two sites.

Also some smaller carnivore species respond to larger carnivores' calls because they may be limited by their presence. Webster et al. (2012) found out that wild dogs moved directly away from lion roars. In the study where lions were displayed to wild dog vocalization they were highly motivated to approach playbacks as lions would kill any wild dogs they could catch (Webster et al., 2010). In cheetahs it was observed that they moved actively from lion and hyena playbacks as well (Durant, 2000). Watts et al. (2010) noted considerable variation among spotted hyena individuals in their responses to lion roars.

2.5 Recognition of interspecific alarm calls

Recognition of alarm calls which are signaling presence of the predator is another type of anti-predation strategy. Alarm calls were detected mainly in social mammal species like primates, squirrels, marmots and birds which gives the appearance of altruism (Sherman, 1977). These calls can contain information about the type of the predator and the level of danger (Manser, 2001). For example, Vervet monkeys (*Cercopithecus aethiops*) give different alarm calls to signal the presence of leopard, eagle and snake (Seyfarth et al., 1980). Meerkats (*Suricata suricata*) call very noisily if the urgency of response is high and if it is low they call more quietly (Manser, 2001).

Some species are able to prosper from the alarm calls of other species. For example they can reduce vigilance in favour of feeding (Bachman, 1993) and the information they obtain from the alarm calls can even save their lives (Templeton and Greene, 2007). The responses to interspecies alarm calls should develop among species that share or have similar predators (Shriner, 1998) and eavesdropping of heterospecific alarm calls should involve learning (Shriner, 1999). Shriner (1999) describes in his study that golden-mantled

ground squirrels (*Spermophilus lateralis*) can learn to associate a novel sound with the appearance of a predator and respond to the novel sound without the predator presence. On the other side Vervet monkeys in the absence of predator learned to ignore other species' alarm calls (Seyfarth and Cheney, 1990). Also similarities in alarm calls of calling and responding individuals may lead to their mutual understanding (Magrath et al., 2009).

Most playback studies have demonstrated that taxonomically related species with similar size may respond to the calls of each other (Carrasco and Blumstein, 2012). This interspecific communication ability can be found mostly between primate species (e.g. Oda, 1998; Ramakrishnan and Coss, 2000; Fichtel, 2004; Eckardt and Zuberbühler, 2004; Kirchhof and Hammerschmidt, 2006), marmots and squirrels (e.g. Shriner, 1998), pikas respond to alarm calls of marmot and ground squirrels (Trefry and Hik, 2009) and among birds (e.g. Griffin et al., 2005; Templeton and Greene, 2007; Coleman, 2008; Goodale and Kotagama, 2008; Magrath et. al., 2009).

Most of the interspecies alarm call studies are focused on primates and birds but studies focused on alarm call recognition among ungulates are completely lacking.

2.6 Interspecific alarm call recognition between different classes of vertebrates

Interspecies eavesdropping can also occur between different classes of vertebrates that are not closely related, for example birds and mammals. Many examples of bird-mammal communication involve primates. One of the most studied cases of mammal-bird signalling is focused on Diana monkeys (*Cercopithecus cambelli*) and different subspecies of hornbills (Rainey et al., 2004a, 2004b). Moreover Diana monkeys are able to discriminate alarm calls of sympatric crested guineafowl (*Guttera pucherani*) (Zuberbühler, 2000). Another examples of bird-mammal alarm call recognition involve e.g. cotton rats (*Sigmodon hispidus*) that eavesdrop on the alarm vocalizations of blue jays (*Cyanocitta cristata*) (Felts and Schmidt, 2010), red squirrels (*Sciurus vulgaris*) recognize jays (*Garrulus glandarius*) alarm calls (Randler, 2006) and meerkats (*Suricata suricata*) respond to fork-tailed drongo (*Dicrurus adsimilis*) (Flower, 2011).

Although most cases involve signalling between birds and mammals, there are some examples of reptiles eavesdropping on bird calls. Marine iguanas (*Amblyrhynchus cristatus*) respond to alarm calls of the Galápagos mockingbird (*Mimus parvulus*)

(Vitousek et al., 2007) and Madagascar spiny-tailed iguanas (*Oplurus cuvieri cuvieri*) increase vigilance after hearing the alarm calls of the Madagascar paradise flycatcher (*Terpsiphone mutata*) (Ito and Mori, 2010).

To date, little is known about eavesdropping of ungulates on bird alarms. Klimšová (2011) found out that roe deer (*Capreolus capreolus*) respond to alarm calls of jay (*Garrulus glandarius*) by flight, increased vigilance or looking in direction of the source of the sound. In Gunter's dik dik it was observed that they respond to alarm calls of go-away bird (Lea et al., 2008).

We do not find many studies focused on alarm call recognition including ungulates. Wildebeest, tsessebe, zebra and especially impala are able to detect baboons' alarm calls from their contest calls because they are at risk from the same predators, including lions and leopards (Kitchen et al., 2010). In another case, a primate responds to the vocalizations of an ungulate; bonnet macaques (*Macaca radiata*) are able to recognize the alarm calls of sambar deer (*Cervus unicolor*) (Ramakrishnan and Coss, 2000).

Carrasco and Blumstein (2012) found that mule deer (*Odocoileus hemionus*) increased its vigilance significantly more after hearing yellow-bellied marmot alarm calls and suggest that relative size differences do not prevent interspecific communication as long as the two species share a predator.

An interesting example of responding to each other's alarm calls was recorded in collared peccaries (*Peccari tajacu*) and South American coatis (*Nasua nasua*) and it is the first report of an interspecific association between an ungulate and a carnivore (Desbiez et al., 2010).

3 Aims of the thesis

Is Blue wildebeest (*Connochaetes taurinus*) able to distinguish the predators' loud calls?

Is there a stronger response of Blue wildebeest to the predator which prefers it as prey?

I supposed that wildebeests should respond to the loud calls of lions and spotted hyenas as wildebeests are dominant large herbivores in savannah and they are the preferred prey of large predators (Estes, 1991). I also expected that they should respond stronger to lions (*Panthera leo*) as they belong to their preferred prey together with other species e.g. gemsbok, buffalo, zebra and giraffe (Hayward and Kerley, 2005) and less to spotted hyena (*Crocuta crocuta*) as they prefer smaller body mass prey like medium-sized ungulates for example impala, kudu, warthog, bushbuck, nyala etc. (Hayward, 2006).

Is Blue wildebeest able to distinguish alarm calls of Greater kudu (*Tragelaphus strepsiceros*)?

Wildebeest and Greater kudu share the same predators and come into contact with each other throughout the habitat. So I supposed that wildebeests are familiar with kudus' alarm calls but the question was whether they recognize it as a reliable indicator of coming threat.

Is Blue wildebeest able to distinguish alarm calls of Helmeted guineafowl (*Numida meleagris*)?

Loud harsh calls of alarmed helmeted guineafowls (*Numida meleagris*) represent typical and conspicuous sounds commonly heard in African bush and savanna. This explosive call accompanying escape behaviour of this species can be heard over long distances and therefore can inform not only conspecific fowls but also broader range of heterospecific eavesdroppers like wildebeests.

What are the other factors influencing the response of Blue wildebeest?

Several factors like season, daytime, group size, sex, habitat, distance to the nearest cover of potential predator, distance to the source of sound and presence of other species may influence the response of blue wildebeest to predator and alarm calls. The aim was to find out, which of these factors affect the response.

4 Material and methods

This diploma thesis was conducted under the project: Role of acoustic signals in prey-predator and predator-predator interactions (CIGA: 51120/1313/3104). During the work on this project I participated in all its parts including research of other species. An analysis of the data on blue wildebeest was my main part in this research project.

4.1 Study area

The research took place in Kruger National Park (KNP). It is situated in South Africa, on the international border with Mozambique and it belongs among the most acclaimed national parks in the world. It covers an area about 20,000 km² and it is 54 km wide and from north to south it measures 345 km. Most of the area is covered by plains and the eastern boundary is formed by low mountains where major rivers drain. Dominant vegetation of the northern part is mopane-veld, and the extensive grassland which dominates the central part is great for viewing large number of game and predators. The southern part covers knob-thorn, bush-willow and marula and the lowest part is rather dense for game-viewing (Braack, 2006). Research was conducted on the extensive area of KNP, mainly in areas around camps Skukuza, Shingwedzi and Orpen (see Fig.3.).

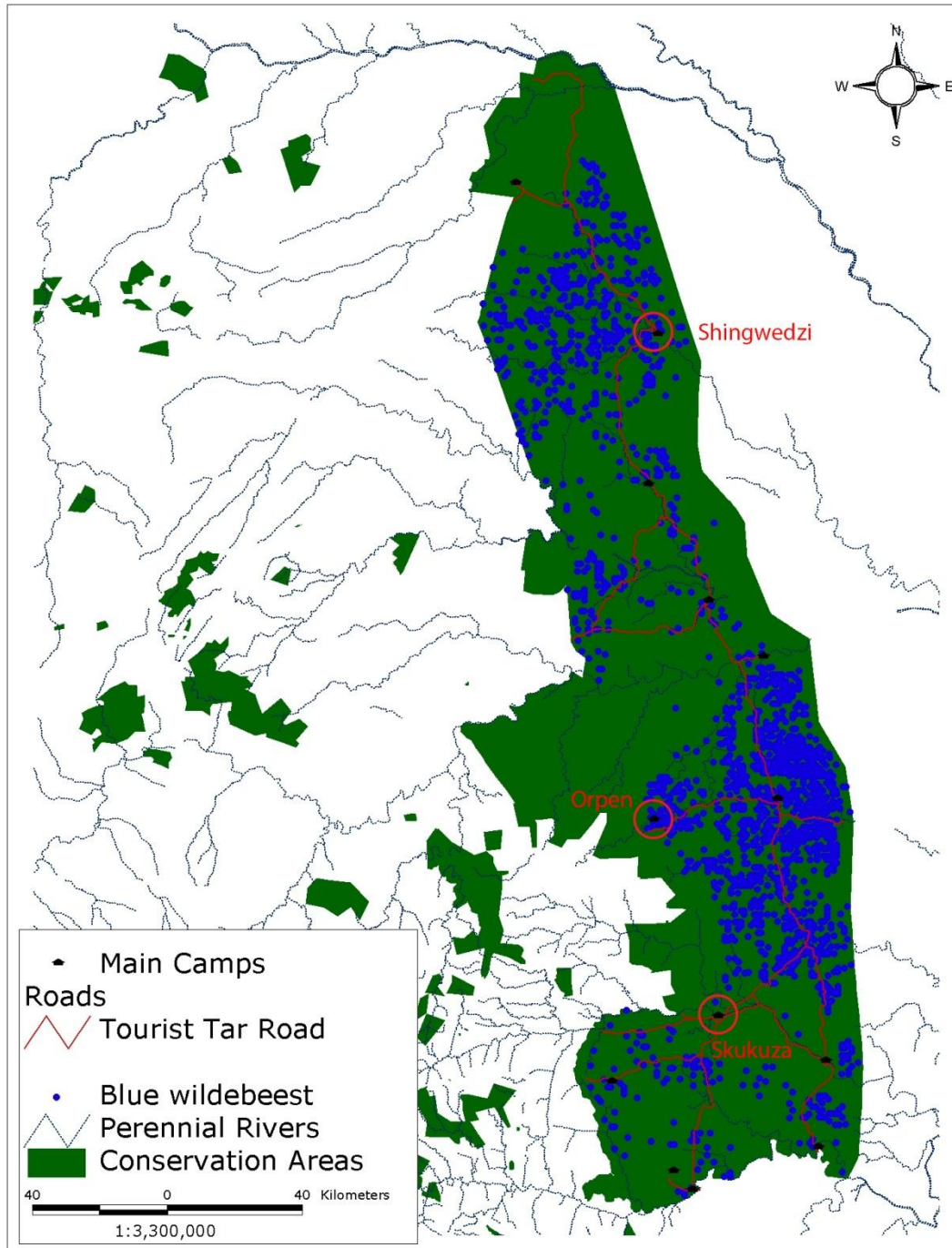


Fig.3. Map of Kruger National Park main camps and blue wildebeest distribution (1990).

During November to February the temperature of the hottest days is above 40 °C so winter months from June to August when the vegetation cover is reduced are better for viewings the game.

It is the home to a rich variety of animal species: 147 mammals, 507 birds, 114 reptiles, 34 amphibians and 49 fish. You can find all the classic African big game there

including elephant, white and black rhino, hippopotamus, buffalo, giraffe, zebra, warthog, many antelope species and also many smaller interesting mammal species. From large carnivores you can spot lion, leopard, cheetah, spotted hyena and African wild dogs (Braack, 2006).

4.2 Animals

I studied blue wildebeest (*Connochaetes taurinus*) recognition abilities to lion and spotted hyena loud calls and greater kudu and helmeted guineafowl alarm calls.

Wildebeests are common large ungulates in KNP. They are the most numerous in the central part of the park that is well suited for various species of grazers. Most recent estimate of their number (year 2010 - 2011) ranges between 6,400 - 13,100 individuals (SANparks 2011).

There are various predator species present in KNP but wildebeests' most common predators are lions (1,620 - 1,750 individuals) and they are also preyed by spotted hyenas (5,340 individuals). Kudus (11,200 - 17,300 individuals) and helmeted guineafowls are common species of the park and they meet with the wildebeests through the study area.

4.3 Playback design

Each experimental playback included control sound and treatment stimuli. At first all the subjects were tested on the response to control sound, non-alarm call of sympatric bird species. The calls of African grey hornbill (*Tockus nasutus*), Swainson's francolin (*Pternistes sawainsonii*) and Cape starling (*Lamprotornis nitens*) were used. Afterwards predator loud calls of lion and spotted hyena or alarm calls of helmeted guineafowl and greater kudu were presented as treatment stimuli.

The experiment composed of 2 minutes of pre-playback (2 minutes before each playback) and 2 minutes of post-playback period (2 minutes after each playback). Treatment stimuli was played approximately 2 minutes after control sound when animals returned back to the routine behaviour like grazing or resting or after terminating of possible response but focal individual did not get out of sight among others.

During the experiments the playback sequences were played in random order. Such matched pair design keep the environmental variables constant (see Kroodsmma, 1989). Each playback was prepared in 2-5 variations. Calls of birds were obtained from

(Chappuis, 2002). Part of mammal calls were recorded by us in KNP and others were acquired from CD Animal calls of Africa. For spectrograms of used predator and alarm calls see (Fig.4.-7.). Sound levels of all calls were standardized using root mean square in Avisoft software (Avisoft-SASLab Pro Software, Version5.1.01). Volume of playbacks was adjusted according to distance.

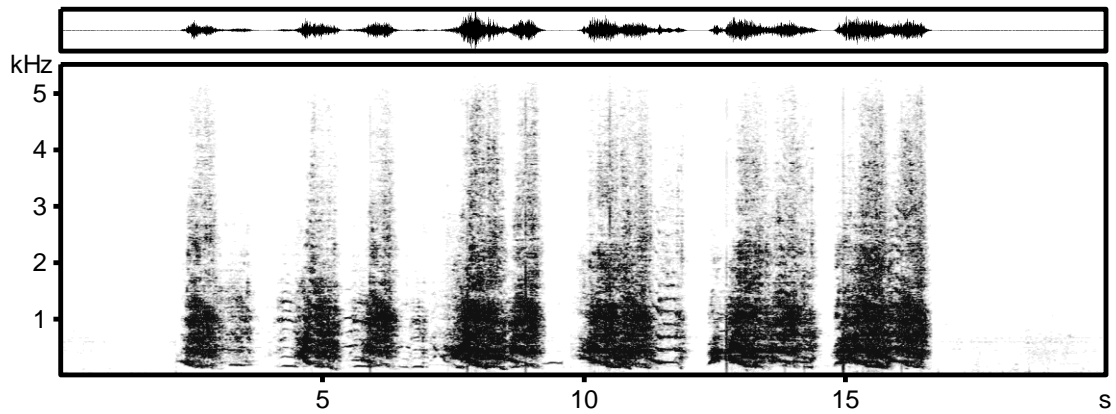


Fig.4. Spectrogram of the lion call.

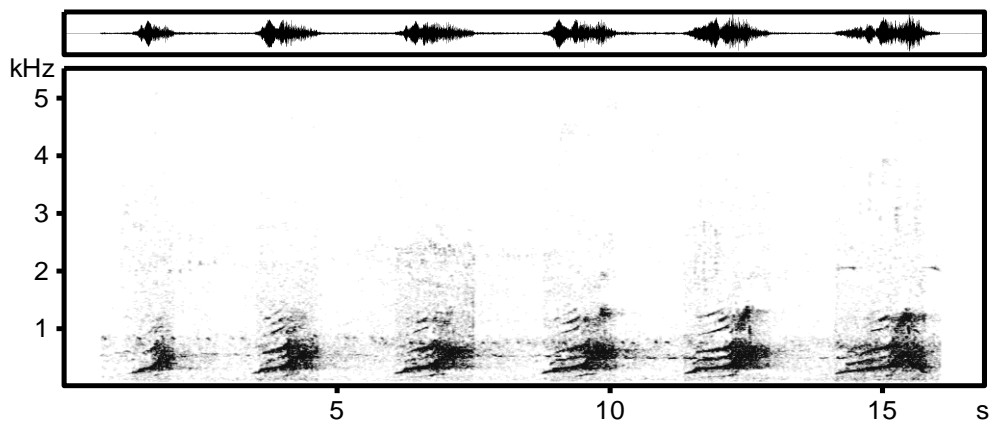


Fig.5. Spectrogram of the spotted hyena call.

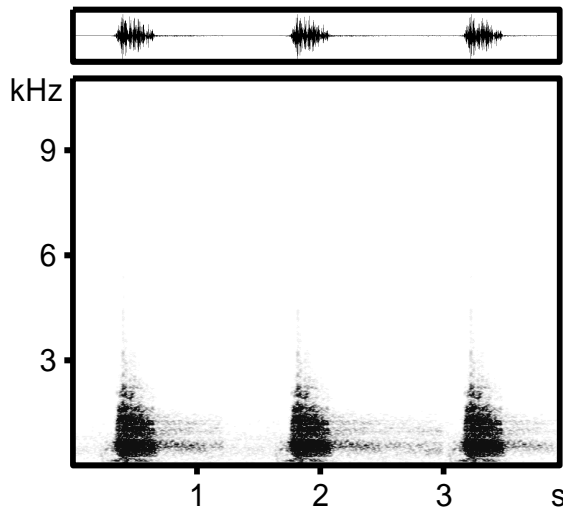


Fig.6. Spectrogram of the greater kudu alarm call.

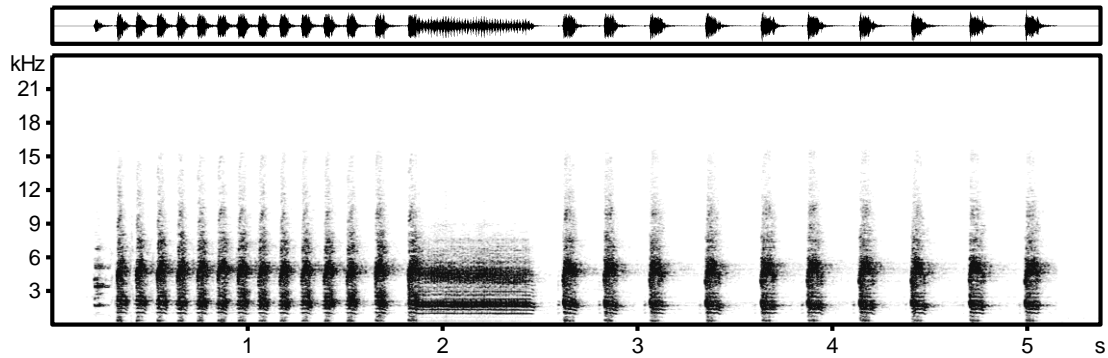


Fig.7. Spectrogram of the helmeted guineafowl alarm call.

4.4 Design of the experiment

The study was conducted in Kruger National Park in the period from July to August 2011 and from October to December 2012 when I was present during the research. Since Kruger National Park is an attractive tourist area, wildebeests were habituated to the presence of vehicles.

KNP was systematically searched for wildebeests both individuals and herds of different size and structure. Animals were sought in different parts of the park to minimize the probability of repetition of testing the same subject and therefore the time and GPS position of each experiment was written down. Other additional data were noted for each experiment and focal individual: date, time, locality, habitat, number of individuals, presence of other species, sex, age, position in the herd, distance to the source of sound

(loudspeaker), distance to the nearest cover. Playbacks were played directly from a standing car after some period of time when the observed animals got used to the presence of the car and returned back to the routine behaviour. Each subject was play-backed only ones. The surrounding was checked against disturbance, natural alarm calls and predators. Experiments disrupted during the playback session were eliminated.

All parts of the playback experiments were videotaped using a Canon digital camera (LEGRIA FS306). The recordings were played through a QTX sound loudspeaker and amplified by an Omnitronic LH-025 stereo mixer linked to Olympus PCM-11.

4.5 Data analysis

I analysed behaviour of selected individual using frame by frame analysis of the video records in program Sound Forge Pro Version 10.0a. It was analysed 30 seconds before and 30 seconds after the start of an alarm and a control treatment. I measured following response parameters: intensity of the reaction, latency of the first and the latency of the most intensive reaction, duration of the first and total duration of the most intensive reaction and the frequency of the most intensive reaction. Responses were divided according to intensity to 4 categories: 0 - *no response*, 1 - *head turn, look* (toward the source of sound), 2 - *head up* (from grazing), *body turn* (toward the source of sound), 3 - *rise* (from a rest position), *escape* (Fig.8.). The strongest response was always recorded, it means if the subject turned the head and then escaped, its response was classified as 3.



Fig.8. *Look* and *escape* response of blue wildebeest (own collection, © Zuzana Panovská).

Both latencies were measured from the beginning of the playbacks (control and treatment). If subjects did not respond to the source of the sound the latency was measured as 30 s. It was subtracted the durations and frequency of response prior to each call from the response after to each call (Kitchen et al., 2010), because some subjects were naturally vigilant before and after the call.

The focal individual was randomly chosen, but most often from the edge of the herd, as they were the most visible and the best traceable among the others during the whole experiment. Only the adult individuals were chosen for the experiment.

4.6 Statistical analysis

Non-parametric statistics Wilcoxon matched pairs test for two dependent variables was applied for a comparison of behaviour between control and treatment stimuli and Kruskal-Wallis test was used for treatment comparison.

Variables such as response of solitary individual compared to herd, presence of other species (yes/no) and daytime period were examined by parametric statistics T-test for two independent samples. Two individuals and more up to 50 were classified as herd. At first I divided daytime according to observation hours to three equal periods of time: early morning (4-9 h), late morning - early afternoon (9-14 h) and late afternoon (14-19 h). Then I tried to put together periods of the day when nocturnal predators as lion and hyena are supposed to be more active and less active: early morning (5-10 h) + late afternoon (16-18 h) and late morning + early afternoon (10-16 h).

Mann-Whitney U test was used for categorical data as intensity of response, small sample size and unbalanced sample size like habitat (open, bush), season (dry, rainy) and sex (male, female). The habitat was classified as open - when animals were situated on the open plain with sparse vegetation around and as a bush when the vegetation was denser with bushes and trees. The season was divided according to the year when the data was collected to dry season - winter (July - August 2011) and rainy season - summer (October - December 2012).

Number of individuals in the herd, distance to the source of the sound and distance to the nearest cover were examined by Pearson rank correlation. Non-parametric Spearman rank correlation was used for intensity of response.

Statistical analyses were carried out in the programme Statistica 12. For all analyses alpha was set at 0.05. All p-values were extracted from two tailed statistical tests.

5 Results

I conducted 83 playback experiments on free ranging individuals and herds of blue wildebeest. All the subjects were tested on the response to control sound - non-alarm call of African grey hornbill, Swainson's francolin and Cape starling and 26 subjects were exposed to the lion calls, 16 to the hyena calls, 14 to the kudu alarm calls and 27 to the guineafowl alarm calls as a treatment stimuli.

36.1% of individuals responded by *head turn* or *look* toward the speaker, 32.5% by *head up* or *body turn* and 30.1% by *escape* or *rise* from the rest position toward the treatment stimuli. Just in one case (1.2%) the subject showed no reaction at all and it was to guineafowl alarm call. After the exposure to control stimuli 59% of wildebeests did not react at all, 27.7% reacted with *head turn* or *look* toward the speaker, 9.6% with *head up* or *body turn* and just 3.6% *escape* or *rise* from the rest position.

After the alarm call of kudu the most common reaction of wildebeest was *escape* or *rise*, whereas it was the least used reaction in other treatment stimuli. When lion playback was played the most often seen reaction was *head turn* or *look* and after hyena and guineafowl call *head turn* or *look* and *head up* or *body turn* were the most common reactions (see Tab.1.).

Tab.1. Number of focal individuals that responded to different treatment according to intensity of response.

Playback treatment	Total number of experiments	Non response	Head turn Look	Head up Body turn	Rise Escape
Lion	26	0	10	9	7
Control bird call	26	15	8	2	1
Hyena	16	0	6	6	4
Control bird call	16	9	3	4	0
Kudu	14	0	4	2	8
Control bird call	14	7	4	1	2
Guinea fowl	27	1	10	10	6
Control bird call	27	18	8	1	0

Comparison of responses to control and treatment stimuli

At first I tested whether the response of wildebeest was different between control and each treatment stimuli. Responses to the call of the lion in comparison to control calls showed significant difference in all tested response parameters. Responses to lion calls showed highly significant intensity (Wilcoxon Matched Pairs Test, $n = 22$, $p < 0.001$) (Fig. 9), shorter latency of the first reaction (Wilcoxon Matched Pairs Test, $n = 26$, $p = 0.002$), shorter latency of the most intensive reaction (Wilcoxon Matched Pairs Test, $n = 26$, $p = 0.026$), duration of the first reaction was longer (Wilcoxon Matched Pairs Test, $n = 25$, $p = 0.006$), total duration of the most intensive reaction was highly significantly longer (Wilcoxon Matched Pairs Test, $n = 26$, $p < 0.001$) and frequency of the most intensive reaction was higher (Wilcoxon Matched Pairs Test, $n = 22$, $p = 0.042$).

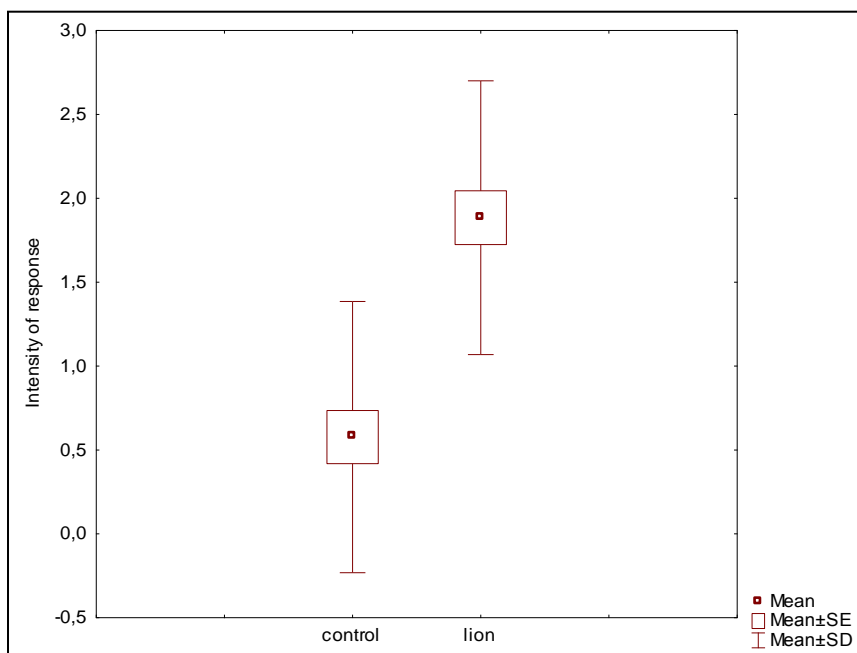


Fig.9. Comparison of the intensity of the response to control and lion call.

Reactions to calls of the second predator, the hyena, were significantly more intensive (Wilcoxon Matched Pairs Test, $n = 13$, $p = 0.001$) and the first reaction lasted longer time (Wilcoxon Matched Pairs Test, $n = 15$, $p = 0.023$). Response behaviour of wildebeests did not reveal significant recognition of hyena calls based on the total duration of the most intensive reaction (Wilcoxon Matched Pairs Test, $n = 15$, $p = 0.125$), latency of

the first reaction (Wilcoxon Matched Pairs Test, $n = 15$, $p = 0.712$), latency of the most intensive reaction (Wilcoxon Matched Pairs Test, $n = 16$, $p = 0.408$) and frequency of the most intensive reaction (Wilcoxon Matched Pairs Test, $n = 12$, $p = 0.480$).

Wildebeests were able to discriminate significantly between alarms of kudu and control bird sounds with greater intensity (Wilcoxon Matched Pairs Test, $n = 11$, $p = 0.013$), duration of the first reaction and total duration of the most intensive reaction were longer (Wilcoxon Matched Pairs Test, $n = 14$, $p = 0.009$, $n = 14$, $p = 0.007$) and frequency of the most intensive reaction was higher (Wilcoxon Matched Pairs Test, $n = 13$, $p = 0.009$). The responses did not differ in the latency of the first reaction (Wilcoxon Matched Pairs Test, $n = 14$, $p = 0.900$) and the latency of the most intensive reaction (Wilcoxon Matched Pairs Test, $n = 14$, $p = 0.451$).

The responses did not differ in the latency of the first reaction (Wilcoxon Matched Pairs Test, $n = 23$, $p = 0.494$) and the latency of the most intensive reaction (Wilcoxon Matched Pairs Test, $n = 25$, $p = 0.192$) to control and guineafowl alarm calls. Discrimination of non-alarm bird call from guineafowl alarm call was based on the intensity of the reaction (Wilcoxon Matched Pairs Test, $n = 22$, $p < 0.001$), duration of the first reaction (Wilcoxon Matched Pairs Test, $n = 26$, $p < 0.001$), total duration of the most intensive reaction (Wilcoxon Matched Pairs Test, $n = 26$, $p < 0.001$) and frequency of the most intensive reaction (Wilcoxon Matched Pairs Test, $n = 21$, $p = 0.018$).

Treatment stimuli comparison

Furthermore I tested whether wildebeests are able to discriminate among different predator calls and alarm call. The reactions did not differ significantly according to the treatment calls based on intensity (Kruskal-Wallis test: $H(3, N = 83) = 3.247$, $p = 0.355$), latency of the first reaction (Kruskal-Wallis test: $H(3, N = 83) = 1.374$, $p = 0.712$), latency of the most intensive reaction (Kruskal-Wallis test: $H(3, N = 83) = 4.161$, $p = 0.245$), duration of the first reaction (Kruskal-Wallis test: $H(3, N = 83) = 0.980$, $p = 0.806$), total duration of the most intensive reaction (Kruskal-Wallis test: $H(3, N = 83) = 5.037$, $p = 0.169$) and frequency of the most intensive reaction (Kruskal-Wallis test: $H(3, N = 83) = 4.559$, $p = 0.207$).

Effect of other factors

Season

I found that none of the tested response parameters was affected significantly by season (Mann-Whitney U Test: intensity of reaction $p = 0.356$, latency of the first reaction $p = 0.965$, latency of the most intensive reaction $p = 0.420$, duration of the first reaction $p = 0.622$, total duration of the most intensive reaction $p = 0.259$ and frequency of the most intensive reaction $p = 0.996$).

Daytime

There was no significant difference in reactions among the early morning, late morning - early afternoon and late afternoon period (Kruskal-Wallis Test: intensity $p = 0.368$; latency of the first reaction $p = 0.878$; latency of the most intensive reaction $p = 0.126$; duration of the first reaction $p = 0.361$; total duration of the most intensive reaction $p = 0.546$ and frequency of the most intensive reaction $p = 0.979$).

There was significantly higher intensity of response during daytime period early morning + late afternoon in comparison with late morning + early afternoon (Mann-Whitney U Test: $p = 0.047$) (see Fig.10.). I did not find difference in other measured response parameters.

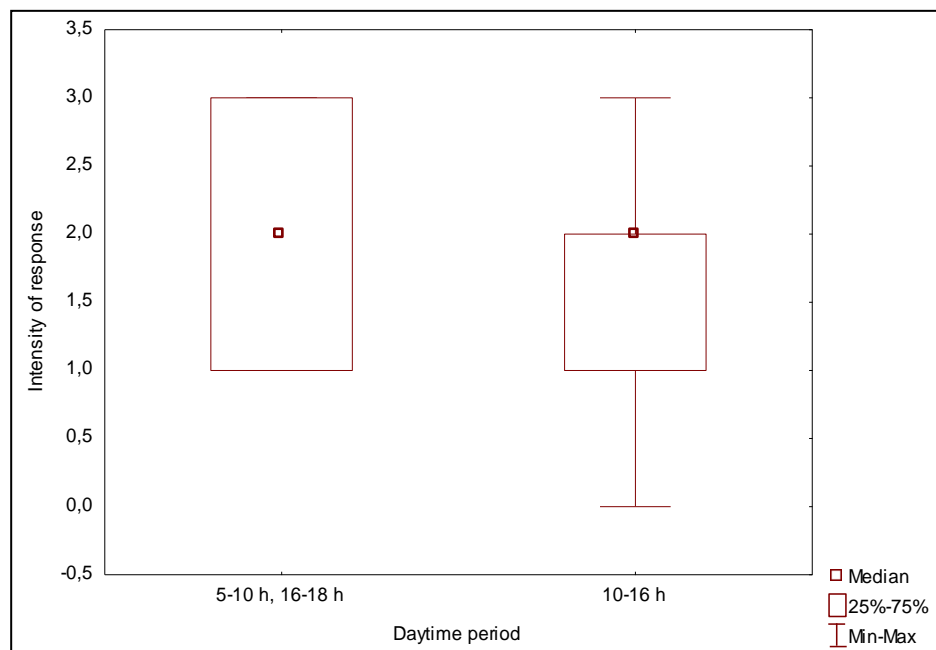


Fig.10. Comparison of the intensity of response according to daytime period.

Presence of other species

Wildebeests exposed to kudu alarms showed shorter latency of the first reaction in the presence of other species (Mann-Whitney U Test: $p = 0.020$) but I did not find this effect in other treatment stimuli (Fig.11.).

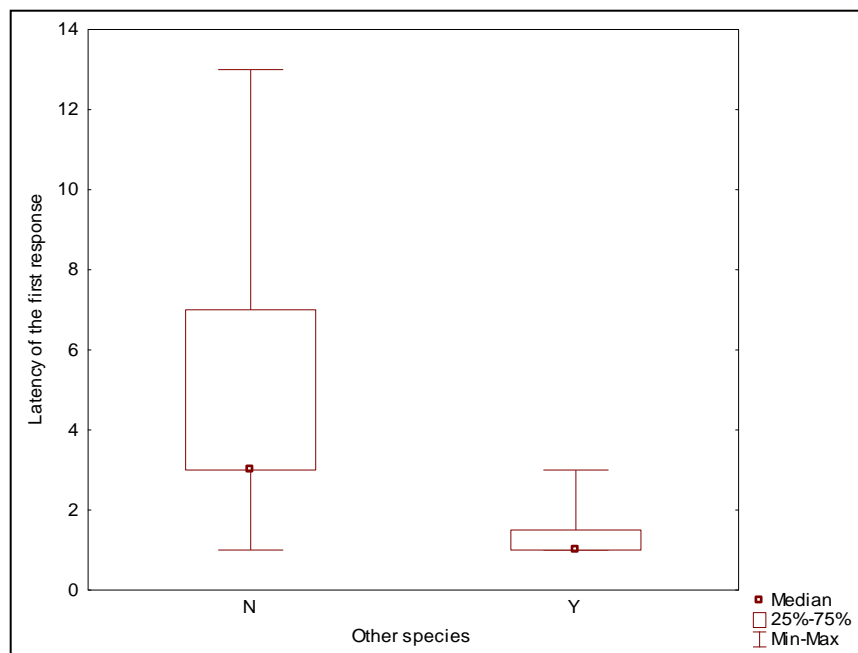


Fig.11. Influence of the presence of other species on the latency of the first response.

Habitat

I discovered that duration of *head up* and *body turn* was shorter in the bush habitat than in open habitat (Mann-Whitney U Test: $p = 0.012$) (see Fig.12.).

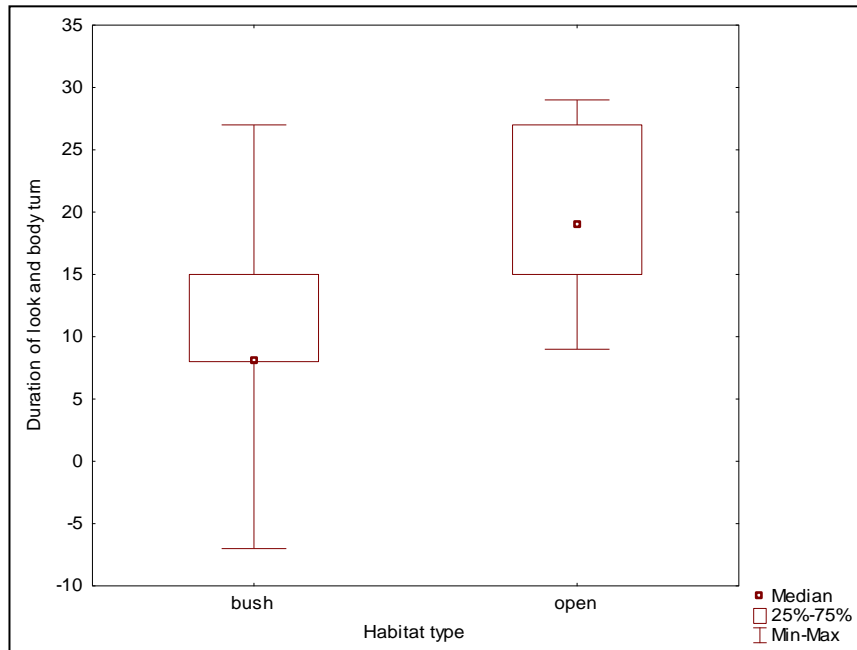


Fig.12. Influence of habitat on duration of the reaction look and body turn.

Distance to the nearest cover

I found out that distance to the nearest cover did not influence any response parameters and the maximal correlation coefficient was $r = -0.121$ (for the intensity of reaction).

Distance to the source of the sound

I tested response parameters using Pearson rank correlation, the maximum correlation coefficient was $r = 0.213$ (for latency of the most intensive reaction), suggesting that there was no effect of distance to the source of the sound on responses.

Size of the herd

I found weak positive correlation between the size of the herd and latency of *head turn* or *look* as the first reaction ($r = 0.421$) (Fig.13.) and *head up* or *body turn* as the most intensive reaction ($r = 0.508$). I also found weak negative correlation between the size of the herd and the duration of *escape* and *rise* as the first reaction ($r = -0.480$) and the most intensive reaction ($r = -0.462$).

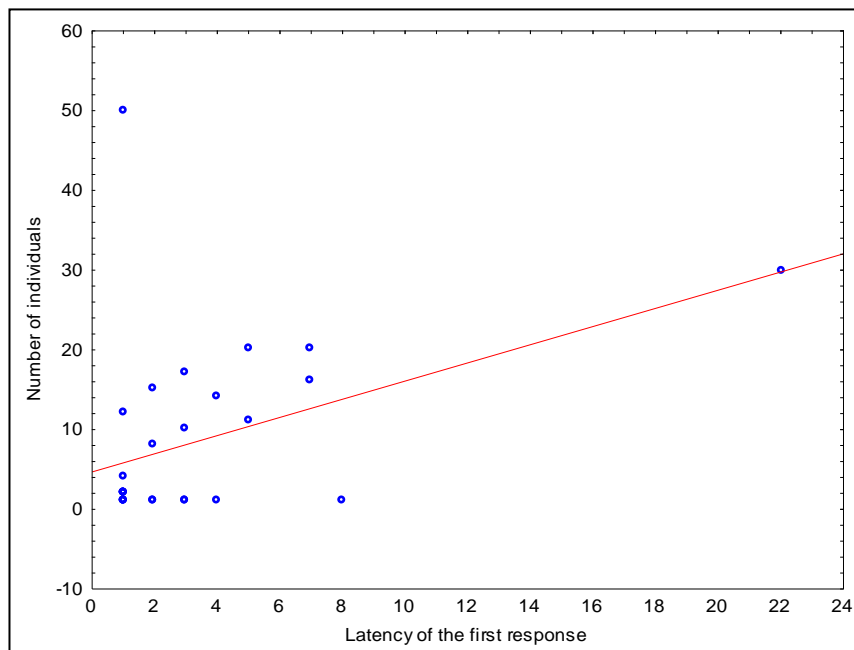


Fig.13. Relationship between the herd size and latency of the first reaction.

There was significantly higher intensity of response in solitary wildebeest in comparison to herd (Mann-Whitney U Test: $p = 0.047$) (see Fig.14.).

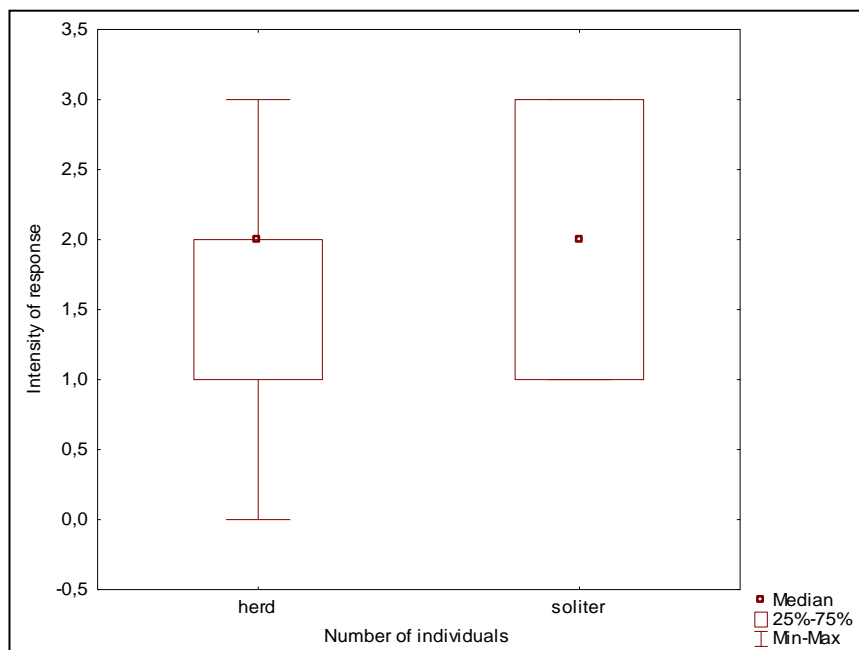


Fig.14. Comparison of the intensity of response in the herd and solitary individual.

Sex

Using Mann-Whitney U Test I did not reveal difference in responses according to sex of the focal individual (intensity $p = 0.802$, latencies $p = 0.964$, $p = 0.369$; durations $p = 0.923$, $p = 0.575$ and frequency $p = 0.923$).

6 Discussion

Predation is a major source of natural selection and shapes the behaviour of prey (Lima and Dill, 1990). The aim of the prey is to maximally reduce the risk of being captured by the predators. Vigilance is the major antipredator behaviour (Lima and Dill, 1990) and it is characterized by the visual scanning that varies with predation risk (Arenz and Leger, 1998). Acoustic signals play a crucial part in the predator detection. The recognition of predator calls and heterospecific alarm calls is highly beneficial antipredator behaviour.

Studies focused on playback experiments when various animal species are exposed to predator calls are becoming more popular. Among the most studied animals belong primates, marsupials, rodents and bird species. But we can find predator acoustic recognition in elephants, smaller predators and water mammals as well.

The ability to recognize predator calls was observed in African ungulates like impalas (Blanchard and Fritz, 2007; Favreau et al., 2013) kudus (Meer et al., 2012) and dik-diks (Coleman et al., 2008). The most common reactions recorded after exposure to predator calls were greater time spent vigilant, the decrease of bite rates and the increase of step rates (but not fleeing).

Wildebeests' antipredator strategies are bunching together, stamping and making powerful shrill alarm calls. The major predators of wildebeests are lions and spotted hyenas, lions being the principal predators in the Kruger National Park (Fay and Greeff, 2006).

Playback experiments study in Kruger National Park was done to reveal whether blue wildebeests distinguish lion and hyena calls and greater kudu and guineafowl alarm calls and which factors could influence responses.

Reactions like *head turn* and *look* toward the speaker, *head up* from grazing and *body turn* toward the source of sound, *rise* from the rest position and *escape* were observed. Three categories of displaying response were determined and it is possible to order them according to intensity. *Head turn* and *look* toward the speaker were considered as the weakest reactions and on the contrary *rise* from the rest position and *escape* as the strongest reaction.

Proportion of intensities of the responses to the treatment stimuli was more or less balanced, nevertheless the most common reaction of wildebeests was the weakest one and

just in one case the subject did not respond at all. More than half of the individuals did not respond to control stimuli and if they did, they responded with the least intensive reaction.

Based on my results wildebeests were able to distinguish the calls of predators like lion and hyena. I did not find any significant difference in the strength of the response when I compared the reactions to lion and hyena playbacks; however, wildebeests significantly recognized lion calls based on all the measured response parameters. This phenomenon could mean that wildebeests recognize better the predator to which they are more vulnerable.

Hyenas and lions occupy the same ecological niche, so they are in direct competition with one another (Hayward, 2006). Interactions between them like following and stealing prey from each other are common. Wildebeests could connect the call of one of the predators with the presence of the other, so not displaying a different reaction between their calls does not necessarily mean that they are not able to distinguish these two predators.

As lions and hyenas are both social animals it would be interesting to test the reactions to a solitary predator like e.g. leopard and see if the social system of the predator has an influence on the responses of the wildebeests.

Many studies revealed that some species are able to distinguish alarm calls of other sympatric species from non-alarm vocalizations. The ability to recognize bird alarm calls is practically unknown in African ungulates. Just one study on Gunter's dik dik revealed that they respond to alarm calls of sympatric go-away bird (Lea et al., 2008). On hearing a go-away bird's alarm call, dik-diks increased their likelihood to run to cover, increased their rate of head turning, decreased their foraging activity and increased their period of vigilance compared with a nonthreatening bird call (Lea et al., 2008).

Helmeted guineafowls often join herbivore herds across the wide range of Africa. This species is known for its offensive calls against predators (Maier, 1982). I confirm that wildebeests recognized this frequently heard alarm call of this common gregarious bird and so can be informed reliably about the potentially coming threat. My results also confirm the findings that interspecies communication occurs not only within taxa, but even between higher taxa like birds and mammals.

Despite the fact that the between taxa recognition of alarm calls is widely studied and in mammals observed mainly among primates, I did not find any study focused on within ungulate species alarm call recognition. My results could be the first to suggest ungulate-ungulate discrimination, resulting from the fact that wildebeests can eavesdrop alarm calls of greater kudu. Ability to recognize kudu's calls can be highly beneficial for wildebeests as kudus prefer to stay in thickets and can spot the predator hidden in the cover lurking for prey and also because they are vulnerable to the same predators.

The power to recognize the potential danger could be crucial to ensure the survival of the listeners. Such an ability of getting additional information about the potential predator's presence by eavesdropping from constantly alert ground dwelling bird or predator sharing antelope could enable more effective anti-predator response and help wildebeests avoid being preyed.

There was no significant difference in the wildebeests' responses to used calls (both predators and alarm) in this study. The same responses of wildebeests to all used treatment stimuli could mirror the similar antipredatory strategy. Wildebeests most often look in the direction of where the sound is coming from trying to find and locate the predator. Only alarm call of kudu was most often followed by more intensive reaction such as rising from the rest position or escape. This might be explained by the fact that predators usually do not vocalize during hunt so hearing the predator's loud call can inform the wildebeests that they occur in their surroundings, otherwise alarm call of the kudu could mean immediate danger signalling that predator was spotted in their vicinity ready for hunt.

Effect of other factors on wildebeests' responses

Antipredator behaviour is commonly considered to be context dependent (e.g. depending on group size, visibility, human disturbance) (Périquet et al., 2010).

Factors like season, habitat, distance to the nearest cover of potential predator, daytime, presence of other species, distance to the source of sound, group size and sex of the focal individual were tested whether they have influence on responses of blue wildebeests to predator and alarm calls.

I expected that responses of wildebeests would be affected by season. One part of the data was collected during dry season when the vegetation cover is reduced so visibility is good and the other during rainy season when the vegetation is dense. Dense vegetation

provides a good cover for potential predators so wildebeests are supposed to be more vigilant during rainy season. Moreover, during the research in Kruger National Park it was observed that wildebeests and zebras were preyed more frequently during wet season, and less during dry season (Funston and Mills, 2006; Owen-Smith, 2008). I found that the responses in the rainy season were more intensive than in dry season, but the difference was not significant. That could be caused by unbalanced sample size: year 2011 (26 experiments) and 2012 (57 experiments) therefore more trails done during the wet season would be needed.

It was revealed that habitat had influence on wildebeest responses. In the open habitat with sparse vegetation the duration of reaction *head up* from grazing and *body turn* toward the source of sound was longer. Studies that have explored the effect of visibility on vigilance behaviour have generally found a decrease in vigilance with an increase in visibility (Bednekoff and Ritter, 1994; Burger, 2001; Pays et al., 2012). Nevertheless Lima (1987) mentioned in his study that visual obstructions in the environment may lead to either an increase or decrease in vigilance, depending on the nature of the environment and how such obstructions manifest themselves in the time budget. Meer et al. (2012) observed that better visibility resulted in an increase in vigilance behaviour in kudus and impalas. Similarly Scheel (1993) discovered that wildebeests scanned less frequently closer to cover such as thick bushes or tall grass and scanned more frequently when cover was limited to short or medium grass, or when cover was discontinuous (stream beds, rocks etc.). Based on my results, wildebeests in the open habitat with sparse vegetation, need to scan for longer periods to check all the possible surroundings.

I found that distance to the nearest cover did not influence responses of wildebeests. Frid (1997) in his study with Dall's sheep came with the same result that distance to nearest obstructive cover had no significant effect on vigilance. However, Burger et al. (2000) recorded that vigilance time in springbok decreased with increasing distance to bushes and that the distance from bushes was the most important variable influencing vigilance. According to Lima (1987) an increase in the distance to cover (safety) may lead to either an increase or a decrease in vigilance, depending upon the situation examined.

According to Kruger National Park rules the wildlife watching is possible only during the day. Therefore we could not conduct the research during the highest hunting activity of nocturnal predators. The research was conducted from early morning hours (5 h) till the evening (18 h) and it was supposed that animals would be most vigilant during early

morning and late afternoon hours in comparison with late morning to early afternoon. According to my results the responses of wildebeests were more intensive than I expected during early morning and late afternoon hours. My results are supported for example by the finding of Meer et al. (2012) who observed that during the early morning (6-9 h) kudus increased their high-quality vigilance and during the later afternoon they seemed to reduce predation risk by reducing the time spent drinking at the waterhole. Scheel (1993) found out that wildebeests scanned the surroundings less during the day and more during twilight because during the day lions are generally inactive and are most likely to hunt at night (Van Orsdol, 1984).

Influence of the distance to the source of the sound was tested as well. It would be expected that with the increase of the distance the vigilance of the focal individual would decrease as it should represent the distance to the potential threat. However, I did not find any difference in the reaction depending on the distance to the source of the sound. Klimšová (2011) studied the responses of roe deer to jay alarm calls and did not find any effect of distance to the source of the sound on reactions either.

I found weak relation between the number of the wildebeests in the herd and the latency of the reaction to the treatment stimuli. The bigger was the herd the later started the first reaction *head turn* and *look* toward the speaker and the most intensive reaction *head up* and *body turn*. I also discovered weak relation between the more individuals being in the herd the shorter was the *escape* and *rise* reaction. The reason why the tested individuals responded later and for shorter time after the treatment stimuli with the growing size of the herd could be explained by the group size effect that could arise from a decreased perception of individual risk and increased ability to detect predators (Childress and Lung, 2003). To detect an approaching predator, an individual can rely on its own monitoring of the surroundings, or it can wait for signals from other individuals (Périquet et al., 2010). Hunter and Skinner (1998) found in impalas and wildebeests that both species showed negative correlation between vigilance behaviour and group size regardless the predation pressure. Underwood (1982) suggested in his study that head up behaviour was negatively correlated with group size. Burger et al. (2000) recorded that vigilance time decreased in springbok with increasing herd size and it was not significant for browsers, but it was significant for grazers.

There was significantly higher intensity of response in solitary wildebeests in comparison with individual within the herd. Solitary individuals are in a greater risk of

being preyed because they cannot rely on dilution effect provided by other group members. They can rely just on their own vigilance and also their antipredator strategies like bunch together, formation of extremely large herds and stamp are efficient and possible only with other herd members. According to Fitzgibbon (1990) Thomson's gazelles (*Gazella thomsoni*) in groups are far less vulnerable to predation than solitary individuals.

Occurrence of other species during the experiments was considered as well. After presentation of kudu alarms, wildebeests responded with shorter latency of the first reaction with other species present. The presence of other species could increase antipredator activity as various preys may attract different predators. Nevertheless further investigation would be needed because of small sample size.

The sex of focal individuals was the last factor that was tested whether it influences the responses of the wildebeests. It seems that reactions were not influenced by sex. In several studies where basal vigilance during grazing was observed it was discovered that females were less vigilant than males. Burger and Gochfeld (1994) observed this phenomenon in wildebeests and many other African ungulates.

In this study representation of females (14 individuals) and males (64 individuals) was not balanced within experiments and in few cases the sex was unknown so farther research would be needed to make some conclusions.

I broadened the knowledge on the predator calls recognition about the fact that other African ungulate - wildebeest also poses the ability to distinguish its natural predators (lions and hyenas). I also found out that they were able to eavesdrop and adequately react to alarm calls of greater kudu and helmeted guineafowl.

Whether the ability to recognize predator vocalization is present from birth or learned is not clear. It seems likely that the recognition mechanism should be experience dependent as e.g. moose ability to reduce responsiveness to extinct wolves returned in single generation (Berger et al., 2007). On the other hand, despite being isolated from predators for 1,200 years in captivity, Père David's deer (*Elaphurus davidianus*) responded to vocalizations of an ancestral predator - tiger (Li et al., 2011). I incline to the opinion that predator recognition ability rises from learning. I think that offspring learn to distinguish predator calls by repeated listening and experience in the group.

7 Conclusions

Using playback experiments I found that blue wildebeests distinguish predator calls of lion and spotted hyena and alarm calls of greater kudu and helmeted guineafowl from non-alarm vocalization of sympatric bird species.

The results showed that there was no significant difference among the responses of wildebeests to different treatment stimuli used, so I did not confirm the hypothesis that there should be stronger response of blue wildebeests to lion. However, focal individuals reacted most intensively to kudu alarm calls, when *escape* or *rise* from the rest position were the most common reactions.

In general the most frequent responses of wildebeests were *head turn* or *look toward* the source of the sound followed by *head up* from grazing and *body turn* toward the speaker.

The finding that wildebeests are able to distinguish predator calls from control calls, contributes to the knowledge of predator recognition in African ungulates. Alarm calls of kudu and guineafowl are reliable predictors of impending threat for wildebeests. Their recognition confirms bird-ungulate and discover ungulate-ungulate interspecies communication.

According to the results, factors like daytime, group size, habitat and presence of other species have influence on the response of wildebeests.

For the future research it would be interesting to test whether wildebeests that live in the area without predators' presence retained the predator recognition ability or react in a different way. Presentation of calls of novel predators could also bring interesting results.

The study is unravelling the field of research which is so far little explored. The understanding of prey-predator interactions could be crucial for launching diverse re-introduction programmes and even acoustic interactions may play an essential role in difficult conservation effort. The results could be also helpful for management and propagation of the park and may contribute to better understanding of behavioural aspects of ecological interactions among keystone species of the park.

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Fig.3. Greater kudu in KNP (own collection, © Zuzana Panovská).

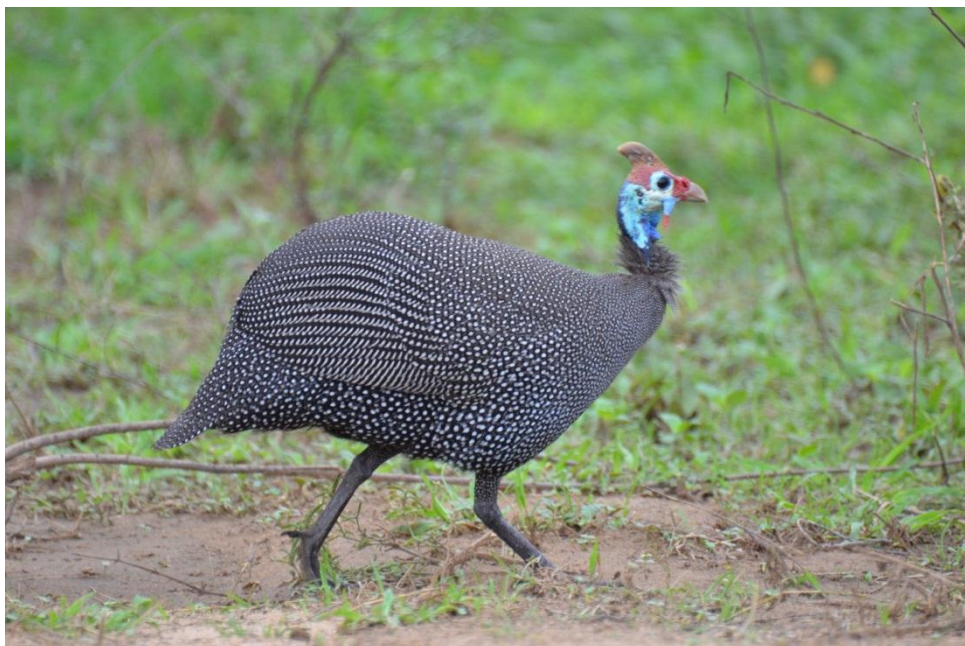


Fig.4. Helmeted guineafowl in KNP (own collection, © Zuzana Panovská).



Fig.5. African grey hornbill in KNP - used as control (own collection, © Zuzana Panovská).



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