Czech University of Life Sciences

Faculty of Tropical AgriSciences

Flight initiation distance – what can tell us about deer farms

Bachelor thesis

Prague 2019

Author: Jan Viktora

Supervisor: Ing. Radim Kotrba PhD.

Declaration

I hereby declare that I have done this thesis entitled Flight initiation distance – what can tell us about deer farms independently, all texts in this thesis are original, and all the sources have been quoted and acknowledged by means of complete references and according to Citation rules of the FTA.

In Prague 24.8.2019

....

Jan Viktora

Acknowledgement

I would like to thank my supervisor Ing. Radim Kotrba, PhD, that he stood by me even though it wasn’t always the easiest. I would like to also thank my dear girlfriend Terezka and my mum, as they always gave me the support that I needed. My classmate and friend Veronika for providing valuable insight and every other person that helped me.

Abstract

Flight initiation distance (FID) is a measurable metric that can describe the general tolerance of animals to distant disturbance and can be used in case of approaching human as a tool to evaluate welfare and tameness of the animals related to man. In this thesis I reviewed and evaluated some of the factors that influence the flight initiation distance (FID) in animals, namely at farmed and free living deer related to various factors. It covered mainly sika deer (*Cervus nippon*), red deer (*Cervus elaphus*) and fallow deer (*Dama dama*) as the most numerous farmed species across Europe and completed by example from other ungulates. Factors studied in relation to FID were group size and sex and age of animals in the groups. Human activity is represented with hunting and non-lethal disturbance. Hunting was proven to extend FID at least for some time after hunting season. Non-lethal disturbance also had an effect and animal habituation to this type of disturbance is also discussed.

Key words: deer, flight behaviour, distance, anti-predatory, flight distance, disturbance

Abstrakt

Útěková vzdálenost je měřitelný údaj, který ukazuje na toleranci zvířete setrvat na místě ve vztahu k přibližujícím se rušivým podnětům, zejména k přibližujícímu se člověku. Díky tomu může být také využita jako nástroj pro zhodnocení welfare a plachosti/ochočenosti zvířat na dané lokalitě. V této rešerši jsem zhodnotil a porovnal některé faktory, které útěkovou vzdálenost ovlivňují, zejména u farmově chovaných a volně žijících jelenovitých. Jednalo se zejména o nejvíce chované druhy jako jelena siku (*Cervus nippon*), jelena evropského (*Cervus elaphus*) a daňka evropského (*Dama dama*), které byly doplněny o další kopytníky. Nějčastěji sledované faktory ovlivňující útěkovou vzdálenost byla velikost skupiny zvířat a věkové a pohlavní složení skupiny. Aktivity člověka byly representovány v rámci lovu a rušení bez ohrožování zvířat. Lov prokazatelně prodlužuje útěkovou vzdálenost minimálně po nějakou dobu po konci lovné sezóny. Neohrožující rušení zvířat mělo také efekt. Bylo také diskutována habituace si ze strany zvířat na tyto podněty.

Klíčová slova: jelenovití, úprkové chování, vzdálenost, proti dravčí chování, úprková vzdálenost, rušení

Contents

1. Introduction

The growing number of deer farms demands that human keepers will have tool to evaluate welfare of deer based on specific farm condition or management. Therefore review focuses on summarisation of factors influencing response/assessing the tameness of farm-kept deer on approaching human observer using so called flight initiation distance.

Flight initiation distance (FID) is a measurable metric that shows the distance between the prey and possible predator before the prey takes flight. First model for FID was economic model by Ydenberg & Dill from 1986 (Ydenberg & Dill 1986). Their work put down foundation for more research and resulting in more sophisticated models. Flight initiation distance is affected by number of different factors, like group size, speed of approach, human caused disturbance etc. (Stankowich 2008). These factors can influence the behaviour of wildlife and farm animals alike.

The majority of welfare issues in deer farms is caused by management, behaviour of humans toward animals or practices like handling, which may be main contributor for stress in deer and subsequently a reason for animal fear or decrease in meat quality prior slaughter (Bornett-Gauci et al. 2006; Hoffman & Wiklund 2006; Williams 2015). It is in farmers utmost interest to keep the stress factors as low as possible. Study of factors affecting FID can than help us better understand how to keep and manage deer in farm conditions.

2. Literature review

2.1 Flight Initiation Distance

Flight initiation distance (FID) or flush distance (Stankowich & Blumstein 2005) is a metric that is defined as a distance between possible predator and prey, when one of them, usually the prey, is threatened or frightened enough to flee to safety (Ydenberg & Dill 1986; Stankowich & Blumstein 2005; Stankowich 2008). Probably the most influential paper about flight initiation distance is *The Economics of Fleeing from*

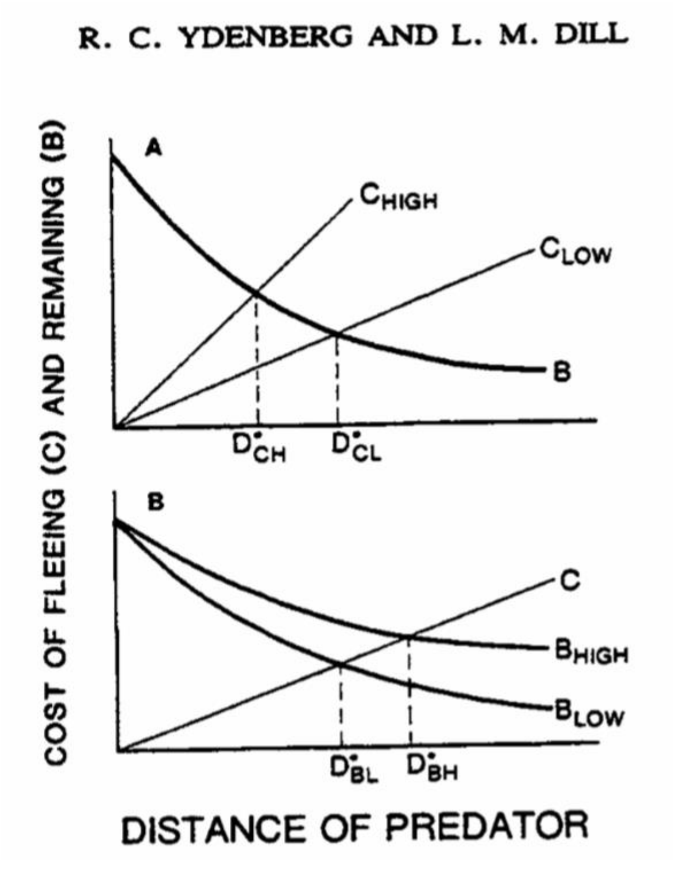


Figure 1: Economic model showing costs and benefits with relation to flight initiation distance. Adopted from (Ydenberg & Dill 1986)

Predators (Ydenberg & Dill 1986), where they put up foundations for future research with their graphical economic model of flight distance (Fig. 1). The hypothesis for the economic model is that flight distance of prey is affected by costs and benefits of fleeing from the threat. (Ydenberg & Dill 1986) and that the escape happens when both costs of fleeing and benefits of staying break even (Ydenberg & Dill 1986; Cooper & Frederick 2007). The main prediction of the model is that animal might delay its escape even after detecting predator, if the added benefits of food gathering are enhancing its fitness (Ydenberg & Dill 1986; Cooper & Frederick 2007). The Ydenberg and Dill, 1986 study is presented in form of four distinct predictions that (1) flight distance increases with risk, (2) flight distance decreases with increasing cost of flight, (3) flight distance depends on alternative prey defence tactics like camouflage and that (4) flight distance is related to group size (Ydenberg & Dill 1986). With enough evidence, Ydenberg and Dill (1986) were able to confirm predictions (1), (2) and (3), but they couldn't make any final statement about prediction (4) since many of the studies presented were of wholly different results concerning relationship between fitness of group, it's vigilance and distance at which they fled. For example Greig-Smith (1981) studied flight distance of

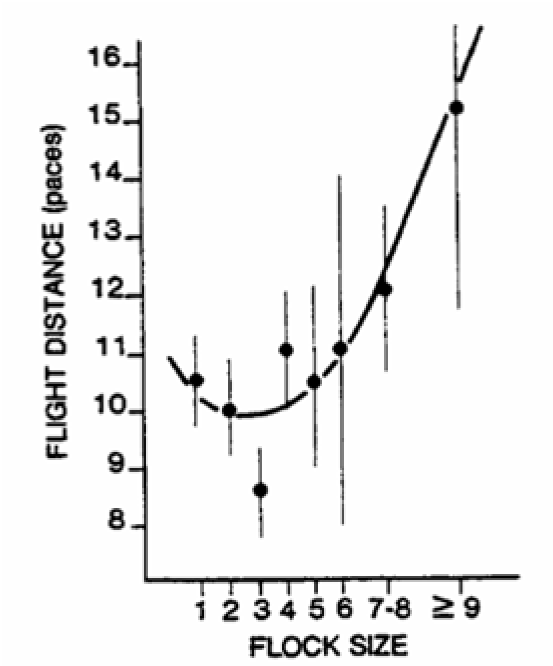


Figure 2: Adopted from (Greig-Smith 1981)

flocks of the barred ground dove (*Geopelia striatus*) in Seychelle islands and found that the distance at which the doves fled appeared to decrease when number of animals increased from one to three, only to start steeply increasing for group sizes of >4 (Greig-Smith 1981)(Fig. 2), showing that there are many variables in case of group size and flight distance of the group (Ydenberg & Dill 1986). Since 1986, Ydenberg and Dill economic model of flight distance has not become obsolete, but rather build upon by other studies. One of the predictions that changed in time is that delaying escape is not optimal for prey and that running immediately after spotting a predator or never trying to run and instead using its own cryptic camouflage is the way to go for prey (Ruxton & Broom 2005;

Blumstein 2010). This is further researched in optimal flight initiation distance model by Cooper and Frederick, 2006. The optimal FID models were built on basis of economic flight distance, but were given a mathematical background and a premise, that prey is continuously assessing new situations and trying to enhance its fitness as much as possible (Cooper & Frederick 2007). In this model, cryptic camouflage changes the probability of survival of the prey (Cooper & Frederick 2007) and the camouflaged prey needs to continuously asses the risk of being discovered by predator (Ruxton & Broom 2005). The contradictions of models and studies that propose that prey takes flight right as the predator is spotted (Coss & Stankowich 2005; Ruxton & Broom 2005) and models that propose, that prey starts to flee when amount of risks and benefits break even (Ydenberg & Dill 1986) or optimal flight initiation distance model (Cooper & Frederick 2007) gave way in last years to flush early and avoid the rush (FEAR) hypothesis (Blumstein 2010). In this hypothesis, Blumstein proposes that "animals will flee approaching predators soon after they detect and identify them as a threat to reduce or minimize ongoing attentional costs of monitoring the approaching predators" and that there is statistical relationship between alert distance (AD, distance at which prey detects predator and orients themselves or looks at them) (Blumstein et al. 2005) flight initiation distance and starting

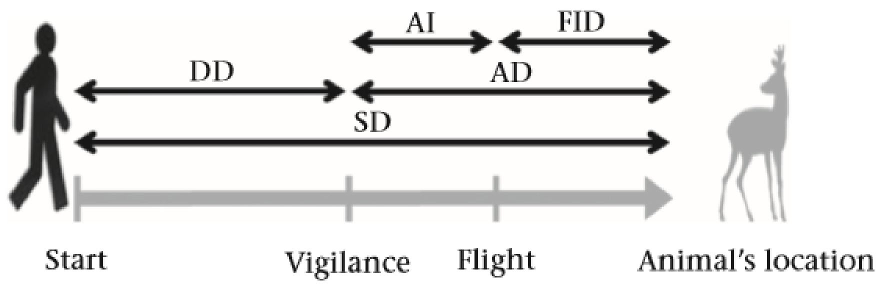


Figure 3: Schematic representation of FID approach showing flight initation distance (FID), alert distance (AD), assessment interval (AI), detection delay (DD) and starting distance (SD). Adopted from (Bonnot et al. 2017)

distance (SD, distance at which the observer starts his approach to the individual) (Fig. 3) (Blumstein 2003, 2010).In a study by Stankowich and Coss in 2005, it has been suggested, that Colombian black tailed deer *(Odocoileus hemionus columbianus*) were more likely to take flight if the approaching observer acted disinterested, this could be interpreted as a prey trying to avoid the chase altogether before the predator spots the prey (Coss & Stankowich 2005). When the prey assess that predator continues the approach towards them, it indicates to prey that it is detected and escape is imminent (Cooper 2005). The FEAR hypothesis was put through test in 2013 analysis of 23 studies that consisted of 5570 individuals from 95 species. The conclusion was that the analysis put enough solid evidence, that results in birds and mammals were consistent with proposed FEAR mechanism. It also identified interspecific variations of flight distance within taxonomic groups, suggesting that different species from the same taxonomic group perceive and assess threats differently and that most species showed large correlation between starting distance and flight initiation distance (Samia et al. 2013). This was further proven by study on yellowed-bellied marmots in Colorado by Williams, Samia et al. in 2014, where they tested relationship between flight initiation distance and alert distance, after accounting for spontaneous vigilance and locomotion in animals. Animals were first observed from afar through either binoculars or spotting scope more than 100

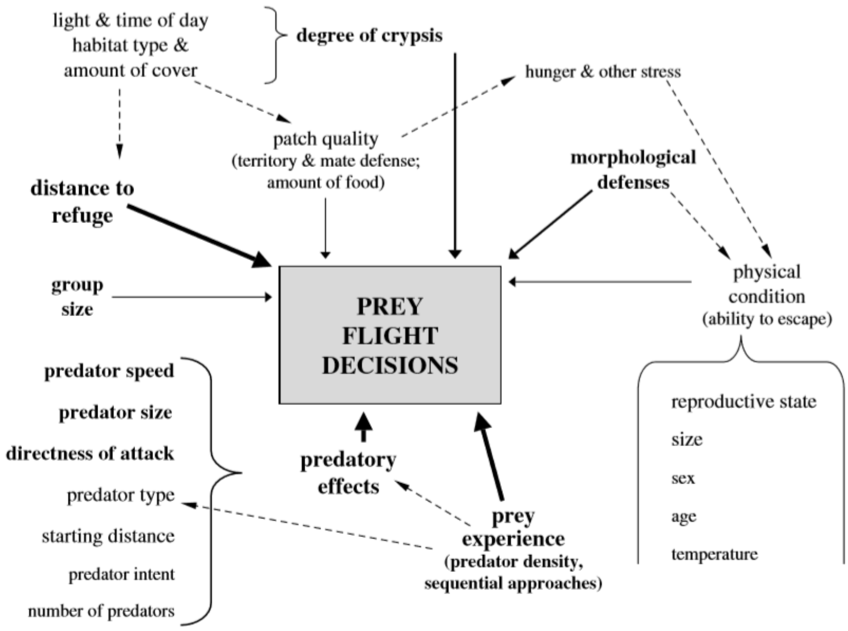


Figure 4: A summary of potential factorss influencing FID. Boldness and size represents relative strenghts of relationships. Dotted lines represent possible indirect relationships. Adopted from (Stankowich & Blumstein 2005)

m from the animals, to not disturb them, to study natural intervals between spontaneous locomotion and vigilance. This dataset was then put through statistical analysis (Williams et al. 2014). The marmots were then tested for flight initiation distance in a standardized way, where once relaxed marmot has been identified, observer sat down for 10 minutes to eliminate any possible effects of arrival. Then a mark was dropped at starting point (estimate for starting distance) and subsequent markers at points where the animal oriented itself towards the observer (estimate for alert distance) and when it began to flee (estimate for flight initiation distance). Once the data were put through analysis, the result of the study was that the relationship between alert distance and flight initiation distance is very strong even after removing the effects of spontaneous vigilance and locomotion. These results show strong support for the FEAR hypothesis that since the prey needs to focus its attention to the incoming predator, it cannot wholly focus on maximizing its fitness through its current activity (Blumstein 2010; Williams et al. 2014). In 2014 the phi (Φ) index was introduced into the FEAR theory as a means of eliminating concerns for statistical inaccuracy from linear correlation, which was used previously on most studies concerning the FEAR hypothesis. These correlation statistics are sensitive to outliers with high leverage and are not appropriate for analysis of relationships constrained in an envelope. The FEAR hypothesis predicts a relationship of 1:1 between alert distance and flight initiation distance. The phi index serves as a way to see how close the observed relationship of AD and FID is from the 1:1 line as a per cent deviation (Samia & Blumstein 2014). Flight initiation distance is influenced by many factors with various relationships as shown in fig. 4 (Stankowich & Blumstein 2005).

2.2 Farm environment

The husbandry practices present or general management at a farm environment can cause stressful nature to animals and can lead to decrease of welfare, production and safety of animals and handlers alike (Rushen et al. 1999) These husbandry practices might be especially stressful to farmed deer, thanks to being a relatively novel farm animal (Diverio et al. 1993) not fully tamed or domesticated like conventional livestock. It has been shown, that even domesticated animals tend to show behaviour present in their wild ancestors – detection and escaping from predators (Lidfors & Jensen 1988) or to human keepers in case of negative welfare stimuli. This process is driven by fear, which is in nature aversive emotional state triggered by external stimuli, motivating animals to avoid possible harmful situations. This includes novel, unpredictable stimuli, like loud sounds or sudden movement, but also negative and unpleasant experiences in farm conditions (Rushen et al. 1999). Aversive behaviour then can be seen in farm animals, if they had previously experienced negative treatment (which can even be benign). This can be seen in a study where Red deer (*Cervus elaphus*) were tested in y-maze preference test. The test consisted of two identical deer crushes placed in an y-maze, each of which led to post-treatment holding area (Fig. 5) (Pollard et al. 1994).

The testing group consisted of 24 castrated yearling males separated in groups 1 and 2 with 12 deer in each. The animals had no previous experience with the testing area prior to the experiment. The testing was done over 5 days in three run periods with one

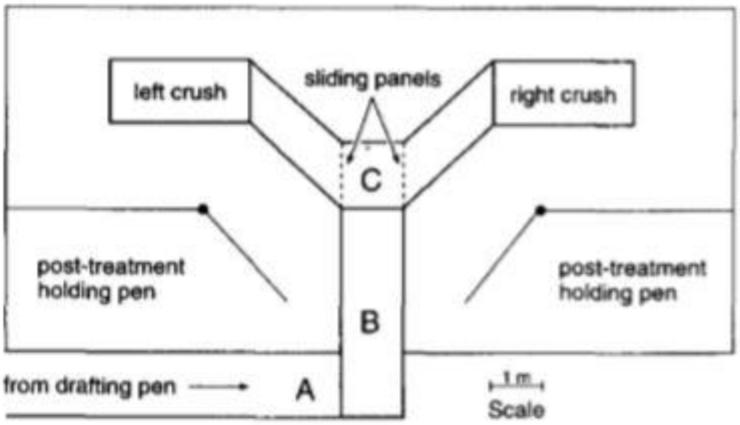


Figure 5: Schematic of the y-maze. Adopted from (Pollarad et al. 1994

period on the first day and two periods on subsequent days, until deer were given 25 runs (Pollard et al. 1994). Treatment in the crush arms were only two, either crush (less then 5s of restraint in the deer crush) or no crush at all, where the deer were able to walk through the crush without restraint. Runs were either "choice" (deer were closely followed until they reached area C (Fig. 5), where they were given a maximum of 30s before being slowly forced into either left or right arm of the maze) or "forced" (deer were followed and pushed forward if they attempted to turn around). Group 1 deer were given only "choice" runs, while group 2 had on a first day a forced run through both arms and then a choice run. Treatments were done so that deer had experienced one of possible side-treatment combinations of left/right arm + crush/no crush. This was repeated twice on day 2 and once on day 3, after that, deer were given choice runs only (Pollard et al. 1994). Once the deer from either group reached 12 successive choices for the same treatment, it was designated "preferred treatment" and the deer were walked through the maze free of any treatment. The result of the study was that group 2 (which had been forced to experience both treatments) showed a significant preference for the no crush treatment, while there was no advantage in giving the deer free choice, although they were more likely to take the other route if they experienced the crush treatment on the first run. Preferences were more pronounced in group 2, where they rapidly learnt the association between sides and treatments, then group 1, where the opportunity of free exploration did not facilitate the learning process (Pollard et al. 1994). Since there were only two possible treatments of possibly highly different aversion, it is possible that had there been more trials and treatments were more similar in aversion, that we could see more stabilized preferences (Rushen 1986).

Similar experiment was done by Grigor et al. (1998) where there was measured the degree of aversiveness in farmed Red deer, where the animals were administered the treatment at the end of simple race way. The experiment was measured in latency of deer in response to different experienced treatments, which were "free run" (control deer that wasn't subjected to any treatment and was let free out of the raceway immediately),

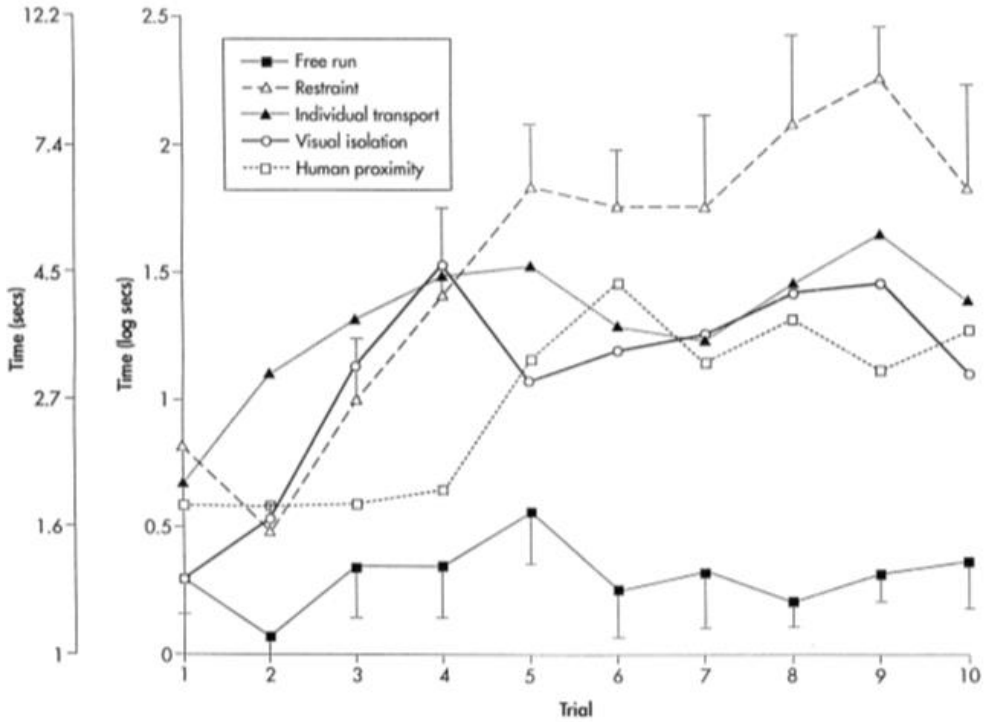


Figure 6: Latency of entering the raceway (sec/log sec) depending on treatment versus number of trials. Adopted from (Grigor et al. 1998).

"restraint" (5 minute restraint in a deer crush), individual transport (deer were loaded into a trailer and then transported for five minutes before let out), visual isolation, where the deer was placed in an empty pen for 5 minutes with no way of seeing the other animals. And human proximity, where 2 handlers entered the same pen as above and stayed there for the 5 minute duration. The results were that there was a difference in latency of entering the raceway depending on the treatment that had been given to the individual, with the control deer being the quickest to enter the raceway, deer exposed to transport, visual isolation and human proximity increased only over the first half of the experiment and the latencies of restrained deer increased until the last trial (Fig. 6)(Grigor et al. 1998).

The way that animals in farm conditions are handled, has clear influence on how the animals perceive the handlers and the level of fear they experience. These aspects are connected to flight initiation distance, as is seen in a study by Hargreaves and Hutson (1990), where they investigated gentling as a possible means of reducing the aversive behaviour in sheep to subsequent handling (Hargreaves & Hutson 1990).

In study of Hargreaves & Hutson (1990) one hundred and eight adult Merino sheep were divided into two groups. One group of 54 sheep was hand fed and every day

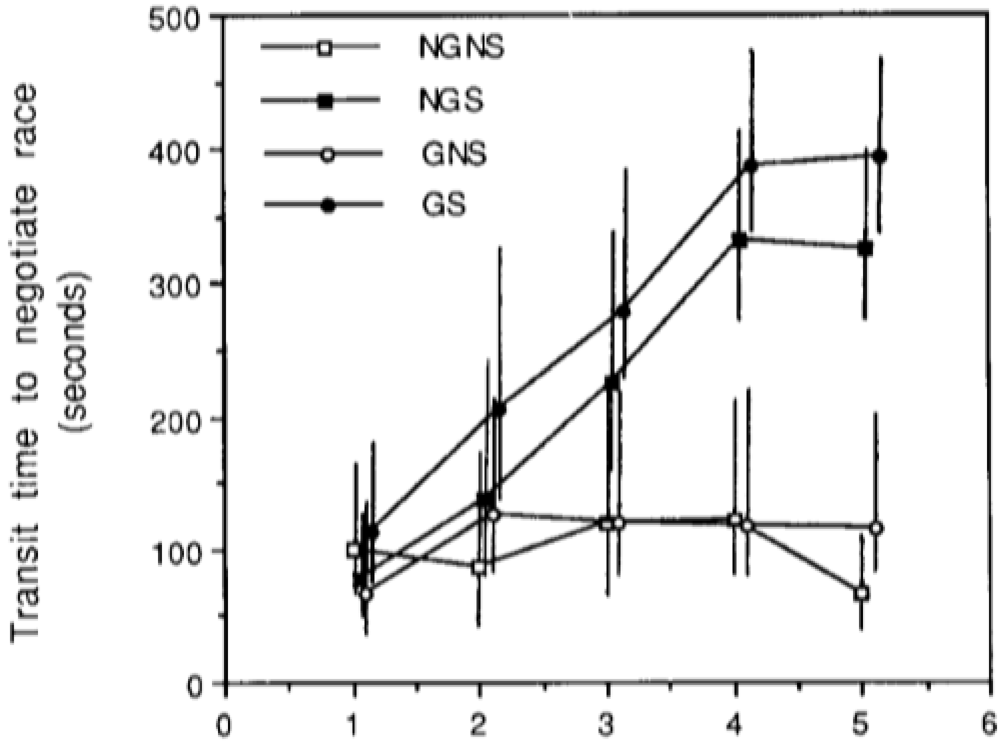


Figure 7: Graph showing transit time to negotiate race (Y-axis) versus time progression in the study (X-axis, numbered in weeks). NG NS – not gentled, not sham shorn; NG S – not gentled, sham shorn; G NS – gentled, not sham snorn; GS – gentled, sham shorn. Adopted from (Hargreaves & Hutson 1990).

for 5 weeks to improve the pasture in 2-ha paddock (gentling group). Second group of 54 sheep were kept in a 7.5-ha paddock and received minimal handling and did not require hand feeding. Then the sheep were divided into four groups of approximately equal numbers, with half and half of gentled and non-gentled individuals (Hargreaves & Hutson 1990). Gentling consisted of one handler patting and talking to an isolated sheep between a set of sheep yards for about 20 seconds. Then the sheep was let go from the isolated space to re-join its flock. Flight distance and heart rates of all sheep were measured before the testing. FID was measured by approaching the sheep at around 1m/s down a 18 m long and 1.5 m wide raceway (Hargreaves & Hutson 1990).

	Not gentled		Gentled	
	Control	Sham shorn	Control	Sham shorn
Flight distance (m)				
Before	4.7[a]	4.1[a]	2.9[b]	2.9[b]
	(0.4)	(0.8)	(0.3)	(0.3)
After	1.3[a]	0.5[b]	0.7[b]	0.2[b]
	(0.3)	(0.2)	(0.3)	(0.1)

Figure 8: Adopted from (Hargreaves & Hutson 1990)

In the experiment of (Hargreaves & Hutson 1990) sheep underwent four different treatments: (1) NG NS - not gentled, not sham shorn (simulated shearing); (2) NG S – not gentled, sham shorn; (3) G NS – gentled, not sham shorn; (4) G S – gentled, sham shorn. Sheep were positioned in a cage at the head of 6 m long and 0.5 wide race which ended in the cage where the flight distance and heart rate were measured. Once the cage was opened, sheep had 3 minutes to enter the race, 3 minutes to pass the half of the race and 3 minutes for the second half of the race. Sheep could go back and forth in a section, but not to previous sections. If the time was up, controller gently pushed the sheep to the next section. Once the sheep was in the cage at the end of the race, the door behind it closed and the door in front opened, then the sheep underwent either 2 minutes of sham shearing or were immediately turned around and allowed to leave the area via the race. This was done over the course of 4 days of each of the 5 weeks. The results were that there was a significant effect of treatment on the transit time of the sheep in the raceway (Fig. 7). The sheep that were gentled had lower heart rates and flight distance before the aversion testing (Fig. 8), but after the testing there was no significant effect of treatment or gentling on heart rate. There was also no effect of gentling in the second series of testing on flight distance, but treatment had significant effect (Hargreaves & Hutson 1990). The daily gentling had considerable effect on reducing the flight distance and heart rate in response to approaching human, this can be considered a taming effect. But after just five trials, the effect of gentling had been obscured. Flight distance was reduced in sheep that had been sham shorn and there was no significant effect of gentling or treatment on the heart rate. This could indicate that the tests themselves had a taming effect. It is important to mention, that while the gentled sheep had longer latency to enter the race, this and the fact that they had reduced flight distance, suggests, that the forcing stimuli had been less potent for the sheep that had been gentled and not be attributed to greater aversion for the treatments (Hargreaves & Hutson 1990). It can be clearly seen in aversion testing, that even the animals have different preferences as individuals, but we can also see that some treatments are much more aversive for the animals then others, this can help us improve the welfare of animals by trying to eliminate as much of aversive practices as possible.

2.3 Description – Cervidae

Members of the Cervidae family are most recognisable by the presence of antlers, which all males have, with only exception being *Hydropotes* sp.(Burton 2002). Females don't usually have antlers, but occasionally develop some form of antlers, usually smaller and/or malformed. Exception being female reindeers (*rangifer* sp.) who have antlers, but smaller and less branched then males (Hall 2005). Antlers have two primary functions, they act as a weapon to protect against predation (Metz et al. 2018) and serve as a means of sexual selection, where males with bigger and heavier antlers tend to be higher in the social hierarchy and of overall better genetic quality. Antlers which are bigger to relative body size are shown to signal increased reproductive capacity (Malo et al. 2005) and increased resistance to pathogens (Ditchkoff et al. 2001). Cervidae are subject to heavily pronounced sexual dimorphism and other then the absence of antlers in females, males are usually about 25% larger than females (Armstrong 2011).

Deer species vary greatly in their size, with the smallest being members of genus *Pudu* at only 35 cm tall and of weight of mere 3,3 to 6 kg (Geist 1998) and the largest *Alces* sp. at almost 2.6 meters at the shoulder and up to 800 kg (Long 2008).

Deer coats are generally coloured from greyish tones in case of elk (*Alces* sp.) to reddish, brown and dark brown. Some species even feature white spots across the brown coat (*Dama dama*, *Cervus nippon*) (Geist 1998). Deer offspring are called fawn and most of them are born with camouflaged coat, with various white spots. (Guinness 1975). In most species these white spots disappear at age of 3-4 months or by the start of first winter. Since most of the members of Cervidae family are hiders in case of their youngs in the first weeks of their life (Chapman 1975), this camouflaged coat helps greatly with blending to the environment and reduces risk of predation.

Females have gestation period of around 180 days in smaller species, to 245 days in larger species and the females usually give birth to one or two fawns. After birth mother hides their offspring in secure place, often in tall grass (Guinness 1975), the mother shows changes in vigilance and flight initiation distance and if feeling there could be a threat to the offspring, relocates it to another save space (Guinness 1975). In this hider period, the mother and offspring are separated most of the time and the mother comes regularly to the place where she hid the young. During the hiding period, the visits from the mother can be as infrequent as only twice or thrice per day (Geist 1974; Guinness 1975; Geist 1998). Unlike other cervidae, *Rangifer tarandus* is of follower type, which are characterized by seasonal movement. Since reindeer travel seasonally great distances, this enables the mother and young to travel with the herd and in case of predation, the mother protects their young. (Geist 1974)

Despite the general thinking that deer are not very vocal, it could in fact not be further from the truth. Members of Cervidae family are very vocal and have wide range of calls ranging from barking relating to detection of predator (Reby et al. 1999) to mating calls during the rut of wide variety of sounds depending on species. Males of fallow deer (*Dama dama*) even have one the highest calling rates of any terrestrial mammal. (Reby & McComb 2003).

Deer are primarily browsing animals; they feed on leaves, shoots, shrubs, soft twigs, fruit, mushrooms and lichens. Since they grow antlers every year, they have very high requirements regarding intake of minerals. (Geist 1998).

2.4 Focused species

In this review we further focus, with some little exceptions, on just three species of the Cervidae family, since these species are the most commonly farmed deer in Europe (Hoffman & Wiklund 2006).

2.4.1 Fallow deer (*Dama dama*)

Fallow deer is a common species native to Eurasia belonging in the subfamily of *Cervinae*, tribe *Cervini* and genus *Dama* (Gilbert et al. 2006). It has been then introduced to many different parts of North and South America, South Africa, Australia and New Zealand (Long 2003).

Male fallow deer is called buck and the female is called a doe. Adult males are around 90 cm at the shoulder and typically weight between 60-100 kg while the females are around 80 cm at the shoulder and typically weight between 30-50 kg. The antlers of fallow deer are shovel shaped (palmate) and up to 70 cm long at the age of 3-4 years (Chapman 1975). Until two years of age, the antler is made of a single spike (Bartos et al. 2002). The coat of fallow deer can be described in four main variations; Brown chestnut colour with white spots and black edge around rump that is replaced by darker winter coat without spots. So called menil colour, which is a brown coat with no black signs and with white spots that are clearly visible even on the dark brown winter coat. Melanistic, which is black coat without any spots and rare leucistic coat, which is true, non-albinism, off white color that becomes pure white for the winter. (Chapman 1975)

2.4.2 Red deer (*Cervus elaphus*)

Red deer is a common species with native distribution ranging from Europe to North Africa and Middle East, since then it has been introduced to New Zealand, Australia, Argentina and Chile (Wilson 2011). Males are called stag and females hind. It is one of the largest deer species, with varied size across 13 subspecies. Average height is 122 cm for males and 114 cm for females at the shoulder. The heaviest being *C. e. elaphus* which can reach weight of up to 500 kg while the *C. e. corsicanus* from island of Corsica weights only about 80 – 100 kg (Geist 1998).

Antlers start growing in the spring and are shed by the end of winter every year. Total length is usually around 71 cm, but especially large antlers can reach lengths of up to 115 cm and 5 kg of weight. Newly forming antlers are covered by velvet in the spring for protection. (Rácz 2003).

Red deer coat is usually reddish-brown through the autumn, winter coats differ from one subspecies to other, with grey or lighter coloured coats present. Males grow specific neck manes during the autumn (Geist 1998).

2.4.3 Sika deer (*Cervus nippon*)

Sika deer is a member of subfamily *Cervinae*, tribe *Cervini* and genus *Cervus* (Gilbert et al. 2006). Sika deer is native to East Asia and can be divided into two distinct types: mainland asiatic sika (*C. n. hortulorum*) with larger Manchurian and Formosan (Taiwanese) forms and smaller sika deer (*C. n. nippon*) originating on the Japanese islands. (Ratcliffe 1987). But since about 150 years ago, Sika deer were introduced into most of the europian countries (Bartoš 2009).

Sika deer are reaching height of 64-100 cm at the shoulder and of weight of 68-160 kg for males of Manchurian form and much lighter weight of 40-70 kg for Japanese sika deer. Thanks to evident sexual dimorphism, females are around 8.7 % smaller on average (Nowak 1991). Sika deer is one of the few species of deer that does have white spots on coat even when adult. The mainland Manchurian subspecies have spots that are larger and more visible, while the Taiwanese and Japanese subspecies have spots almost invisible. The coat is usually of darker tones of brown to black, occasionally white. The coat becomes darker and rougher with spots hardly visible. Males also grow mane on the back of the neck (Nowak 1991).

2.5 FID in farm environment

Since there is a rising trend in deer farm numbers and increasing demand for venison (Hoffman & Wiklund 2006; Kuba et al. 2015), deer farms are more and more common in today's world. Flight initiation distance can serve us as a tool for evaluating tameness and welfare of the animals or response to approaching human observer, since the FID is significantly lower in tamed individuals. This can be seen in study by Pelikan in 2015, in which they studied if FID can be used to evaluate effects influencing tameness (Pelikan 2015). The study was done on three species of deer in farm conditions: Red deer,

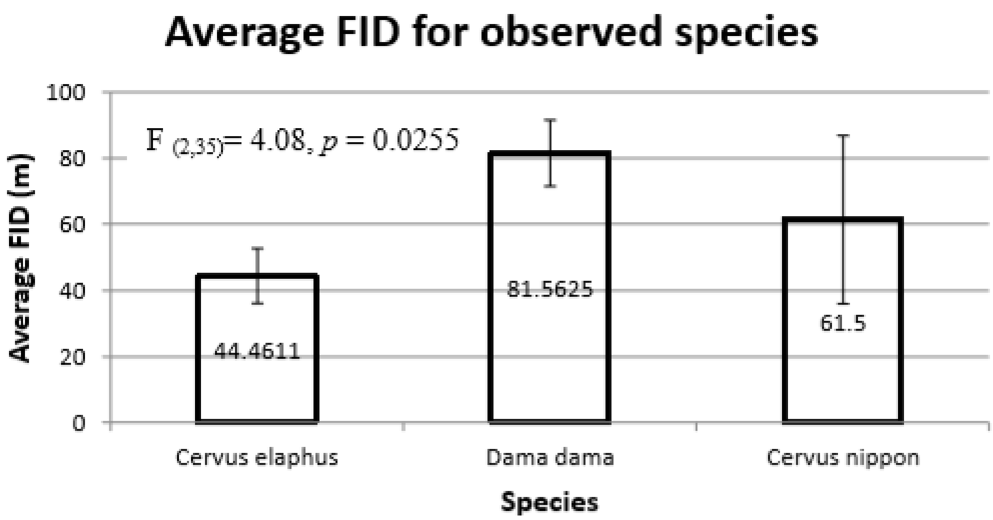


Figure 9: Adopted from (Pelikan 2015)

Sika deer (*C. nippon*) and Fallow deer (*Dama dama*). The farms were in 4 regions of Czech Republic and had comparable habitat – open areas with few solitary trees. There were 41 total measurement from 16 farms. The results were that from the three deer species, average FID was shortest for the Red deer (44.46 m), highest for Fallow deer (81.56 m) and Sika deer in the middle with 61.5 meters (Fig.9). Presence of the tame individual was also considered, showing that when the tame animal was present in the group, the animals tend to let the observer come closer. If the tame animal was present, the average FID was 21.07 meters, versus absence of the tame animal, where groups took flight on average at 103.94 meters (Fig. 10), showing that tame individual can influence behaviour of whole group (Pelikan 2015). This is still clearly visible even in interspecies behaviour: Red deer had average FID of 30.22 meters if tame individual was present

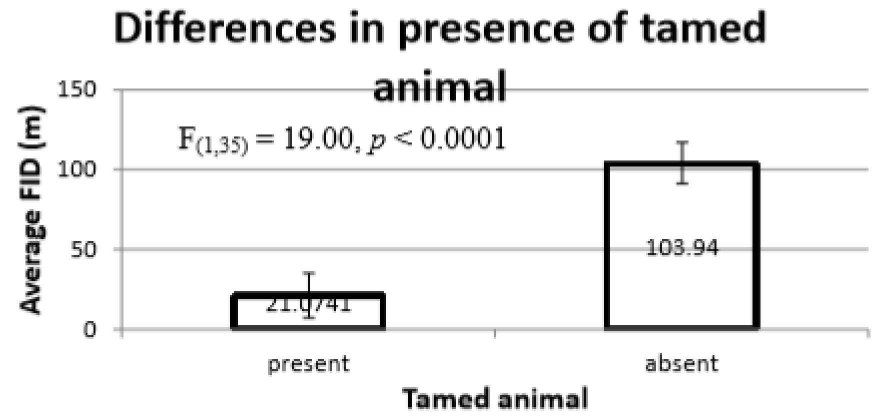


Figure 10: Adopted from (Pelikan 2015)

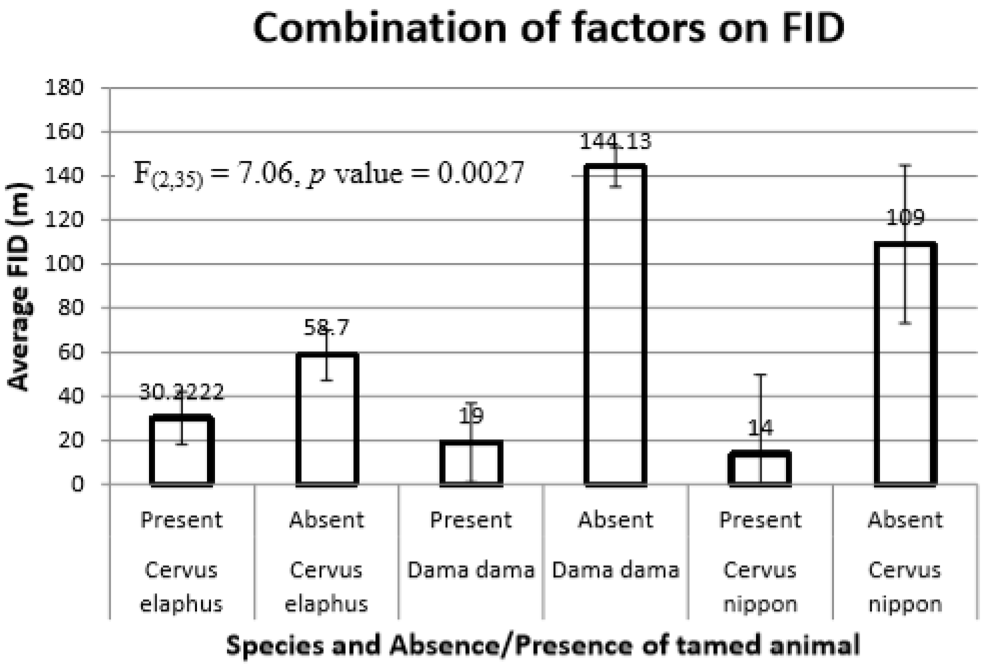


Figure 11: Adopted from (Pelikan 2015)

versus 58.7 meters if tame individual was absent. Fallow deer had average FID of 19 meters if tame individual was present versus 144.13 meters if absent. Tame Sika deer couldn't be found in the two trials, with the other two being one FID of 14 meters and other of 109 meters (Fig. 11) (Pelikan 2015). These results show that there is significant influence on FID through the presence of tame individual which then influences behaviour of the whole group.

2.6 Group size and composition

Large number of studies on ungulates has been done to measure the effect of group size on FID with various outcomes (Stankowich 2008). The effect of group size on the FID is wildly varied across taxa and species with some showing negative effect, some positive effect and some showing no difference between grouped and solitary animals (Stankowich & Blumstein 2005).

When Stankowich and Coss studied effects of predator behaviour and proximity on risk assessment on Colombian black-tailed deer (*O. h. columbianus)*, they found out that group size had negligible effect on FID, but had an effect on assessment times. Deer, when in larger groups, were more vigilant and had lower risk assessment times (distinct alert postures that permit measurement of the actual time spent attending to the approaching threat) and that flight can be initiated by one individual in the group, while other individuals in the group follow (Coss & Stankowich 2005). On the contrary when Recarte et al. (1998) studied flight responses in fallow deer kept in enclosed park population, they found out that larger groups (>5) of animals took flight in 37.1% of time, versus the 41% for small groups of 2-5 animals and 42.9% in solitary deer. Female groups had also largest chance of fleeing versus male, juvenile or mixed groups (Recarte et al. 1998).

Bonnot et al. (2017) observed roe deer (*Capreolus capreolus*) and how they adjust their flight behaviour to the perceived trade-off between risk and reward in Aurignac, France. In this observation, larger groups detected threat sooner than individuals (Fig. 12) (Bonnot et al. 2017), giving support to “many eyes” hypothesis that suggests, that large groups are better at detecting threads due to increased collective vigilance (Lima 1995).

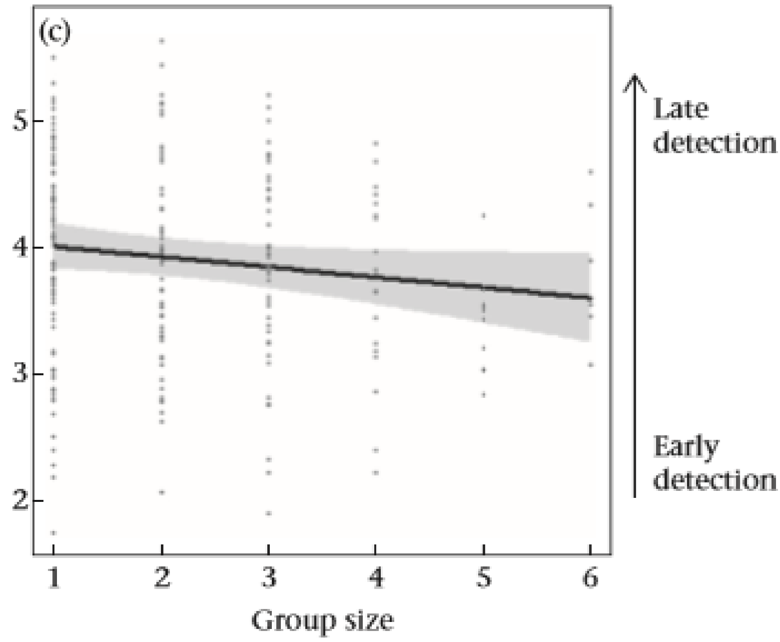


Figure 12: Detection delay (Y-axis) versus group size (X-axis). Adopted from (Bonnot et al. 2017)

This hypothesis’s main premise is that as the group of animals is getting bigger, they are more able to check and scan the environment for any predators. This is based on the assumption, that animals can collectively detect predators by monitoring vigilance of their groupmates, which means that an individual can spend more time foraging, since there could be only one member of the group to perceive threat to alert the whole group. But this hypothesis has been only weakly supported, since the behaviour of monitoring doesn’t seem to work and the basics of the premise could be expressed through different hypothesis like dilution effect (Lima 1995). Dilution effect is a theory present in groups of animals, that any given predator can only capture one member of the group at a time, diluting chance of being captured between the groupmates in the group (Lehtonen & Jaatinen 2016). On the other hand, when Taraborelli et al. (2012) studied groups of guanacos (*Lama guanicoe*) and their antipredator mechanisms, they found out that detection of predator and FID increased in relation to bigger sizes of the group, suggesting that cooperative vigilance helps groups to avoid danger posed by predator, rather than dilution effect, which doesn't seem to be present (Taraborelli et al. 2012). (Donadio & Buskirk 2006) in their study on guanacos and vicunas (*Vicugna vicugna*) found no correlation between group size and FID.

The results in the research of relation between flight initiation distance and group size can be even so varied that we can observe three different results on the same species. While in a different populations and areas, in quite similar level of exposure to humans and hunting. Aastrup (2000) found that reindeer (*R. tarandus)* were more prone to longer FID in large groups (group average of 145.6 m versus 93.4 m for individuals) (Fig. 13) and that the most vigilant were groups with calves, with no difference between male and female groups (Aastrup 2000). Other study on reindeer shows that FID decreased with group size and composition regarding sex and age did not influence FID and that larger groups are less vigilant (Reimers et al. 2006). While study by Colman et al. (2001) found no difference in any response distance in relation to group size of wild reindeer. They

	Mean	Upper 95% confidence limit	Lower 95% confidence limit	Significance
Group	145.6	159.9	132.6	0.0001
Single	93.4	111.3	78.3	
Isortoq pop.	129.5	147.0	114.0	0.0108
Akia pop.	103.6	118.4	90.6	

Figure 13: Adopted from (Aastrup 2000)

also didn't find any difference in response in relation to group composition (Colman et al. 2001). These results are proving to us why there is currently no consensus regarding relationship between group size and flight initiation distance. Larger groups could have greater flight initiation distance because the probability of having one flight prone individual is greater in larger groups (Stankowich & Coss 2007) while smaller groups could have greater flight initiation distance thanks to the lack of "dilution effect" observable in larger groups. This may point to the theory that effects of group size are not species specific and are instead dependent on factors like history of the population, type of habitat, season and level of exposure to humans (Stankowich 2008).

Although the topic of how group composition affects flight initiation distance is better observed then group size, it is still not clear. We can generally say that sex has consistent effect on flight initiation distance. Male groups usually have the shortest FID, which is even more pronounced when in rut or guarding females (Stankowich 2008).

Females on the other hand are most likely to flee sooner than male or mixed groups (Coss & Stankowich 2005). This is especially true for females with young who are more vigilant and flee sooner and further (Colman et al. 2001), this same behaviour can be seen in rut season (Ciuti et al. 2008). The behaviour of fleeing sooner, being more vigilant and anxious, observable in females with young can be tracked to maternal instincts of the mother to protect her young (Guinness 1975; Stankowich 2008). Young animals are at bigger risk of predation (Blanco et al. 2011) and the greater FID could be reasoned that younglings don't have yet developed escape tactics, so the mother encourages the young

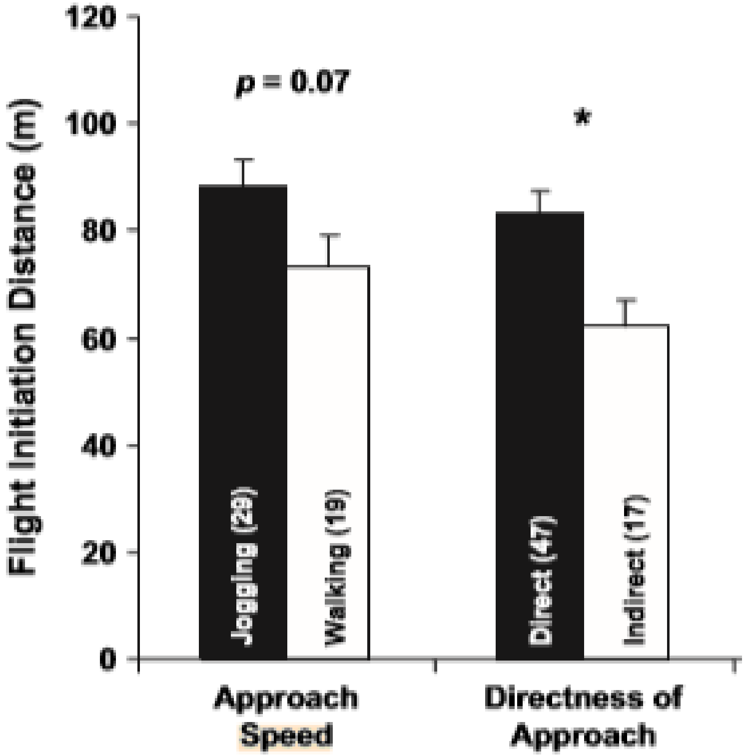


Figure 14: Adopted from (Stankowich & Coss 2006)

to flee earlier to have enough time to get to safety (Stankowich 2008).

2.7 Speed and directness of approach

The speed at which the predator approaches the prey has an effect on flight initiation distance (Stankowich 2008). In 2006 study by Stankowich and Coss on effects of predator behaviour and proximity on risk assessment done on Colombian black-tailed deer the speed at which the observer approached the animals played significant role. The approaches were of varied types, walking and jogging and approaching on a direct line to the approached animal and indirect approach, where the observers point of approach was approximately 30 m to either side of the approached animal and gaze averted approach, where the observer averted direct eye contact by looking away on the ground from the animals (Stankowich & Coss 2006). The results were that the speed and directness of approach played significant role in FID. When the observer was jogging, the average FID was 88 ± 5 m, while walking FID was 73 ± 6 m at average. When the animals were approached on direct line, the average FID was 83.4 ± 4 m, while on indirect approach FID was 62.5 ± 5 m (Fig. 14) The averted gaze approach (FID of 63.8 ± 8 m) was deemed statistically insignificant. These results are corresponding to the predictions and show that with faster and more direct approach, animals tent to perceive it as bigger threat, than when approached indirectly and slowly, indicating that this kind of predatory behaviour is threatening to the prey (Stankowich & Coss 2006). ¨

2.8 Human disturbance

Disturbance of wildlife and farm animals is prevalent in today's world, be it fragmentation of habitat by roads old and new, land and air vehicles, new buildings and settlements, tourism and even ecotourism. All these factors contribute to how the behaviour of animals changes when they meet humans and human infrastructure.

2.8.1 On-foot human disturbance

Generally the humans on foot are most evocative for the animals to be perceived as a threat (Stankowich 2008). When tourist paths are present in the area, the behaviour of animals changes as they try to avoid areas of disturbance. This can be seen in study by Sibbald et al. in 2011, where the studied how Red deer responded to regular disturbance by walkers on the walking path (Sibbald et al. 2011). The study was done in Mar Lodge Estate area in Grampian, Scotland. The area covers 29 340 ha, or 293 km^2 and at the time of study, estimated 4000 Red deer were present in the reserve. The study site was Glen Lui, which has a walking track and automatic counter of walkers that is recorded, approximately 20 000 walkers frequent the track every year. The recorded data were obtained via GPS (Global Positioning System) collars, that were fitted to eight mature

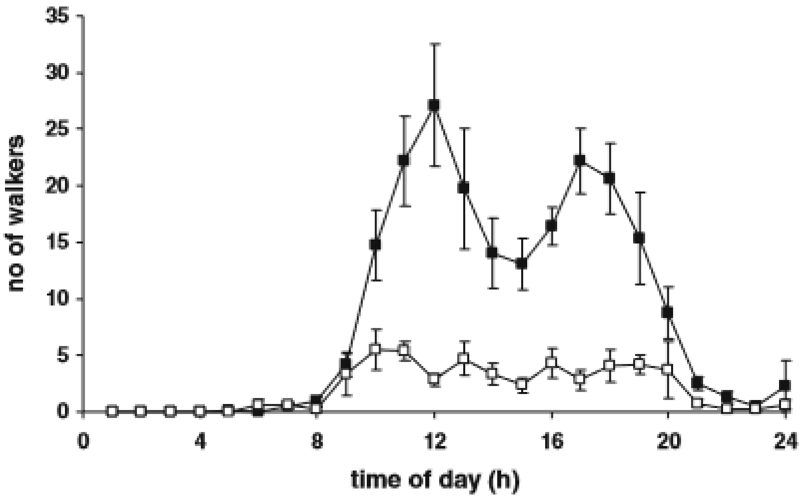


Figure 15: Wednesday (□); Sunday (■). Adopted from (Sibbald et al. 2011)

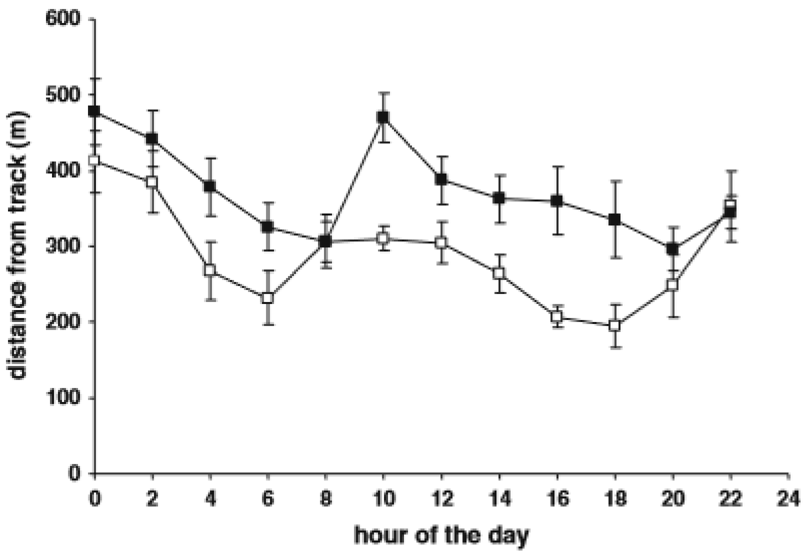


Figure 16: Wednesday (□); Sunday (■). Adpoted from (Sibbald et al. 2011)

Red deer males with four stags at the end of March in 1998 and four stags at the end of March in 1999, collars were removed approximately after 11 months in each case. As the deer had no indication of what day it is, except the amount of walkers, Sundays and Wednesdays were chosen, as any differences in behaviour would most likely be because of number of walkers observed by the deer. The results were that the counter showed on average four times the number of walkers on Sundays than on Wednesdays (204 versus 49.4) with 97% walking between 0800 and 2000 hours each day (Fig. 15). Distance of the deer from the track was also greater on Sundays than Wednesday (average 371 m versus 286 m) (Fig. 16) (Sibbald et al. 2011)

2.8.2 Hunting

Flight initiation distance is clearly influenced in areas where hunting activity is present, but there are some studies that present no effect or just very little (Stankowich 2008). In 2004 Buskirk studied how does poaching affect flight behaviour in guanacos and vicunas in three reserves, two of them where poaching was present and one where poaching was not present, in western-central Argentina. The data were gathered between June – August on 9 transects of different lengths of 4.9 to 26.5 km from vehicles. The recorded data consisted of three flight responses – staying, walking away and fleeing. The prediction was that animals in areas with poaching activity will be more wary, FID will be greater and frequency of fleeing will be increased in comparison to areas with no

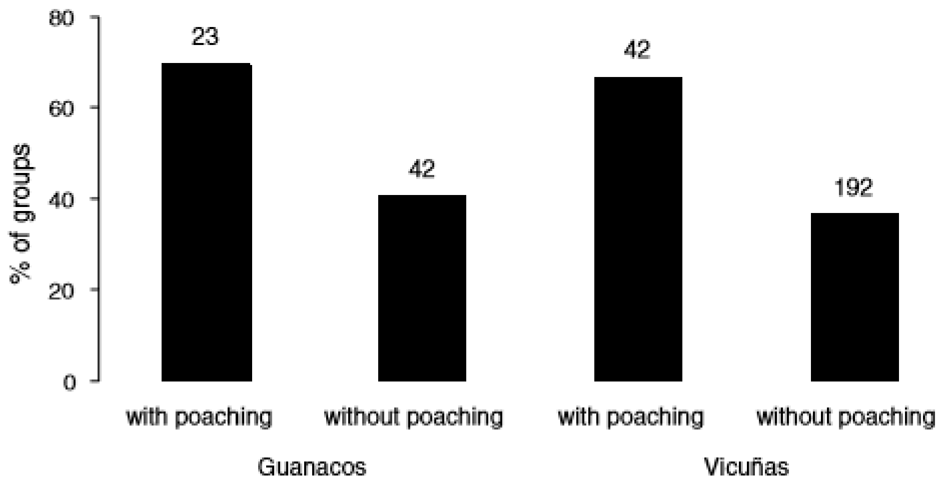


Figure 17: Percentige of groups that would take flight when approached. Adopted from (Donaldio & Buskirk 2006).

poaching present (Donadio & Buskirk 2006). In the end, the information was collected on 234 groups of vicunas and 65 groups of guanacos. There was no difference between guanacos and vicunas in frequency of fleeing and walking/staying. The median time to first flight was much shorter in areas with poaching then without, this was less pronounced in guanacos. The same result was true for median flight distance, with areas with poaching having greater flight distance for vicunas, but not as big of an impact on guanacos (Fig. 17) (Donadio & Buskirk 2006). Experience with hunting plays a role in affecting flight distance. We can see that in a study by Aastrup (2000) on Greenland Caribou (*R. tarandus*). The study was done in West Greenland during calving, summer and after hunting in 1997-1998. There were two populations studied, the Isortoq and Akia. The results were that animals showed increased vigilance, flight initiation distance and fled further just after hunting season, comparable to behavior during calving season (Fig.

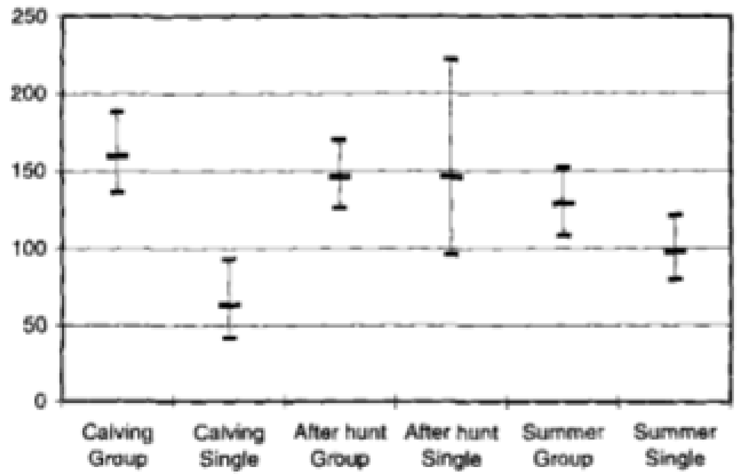
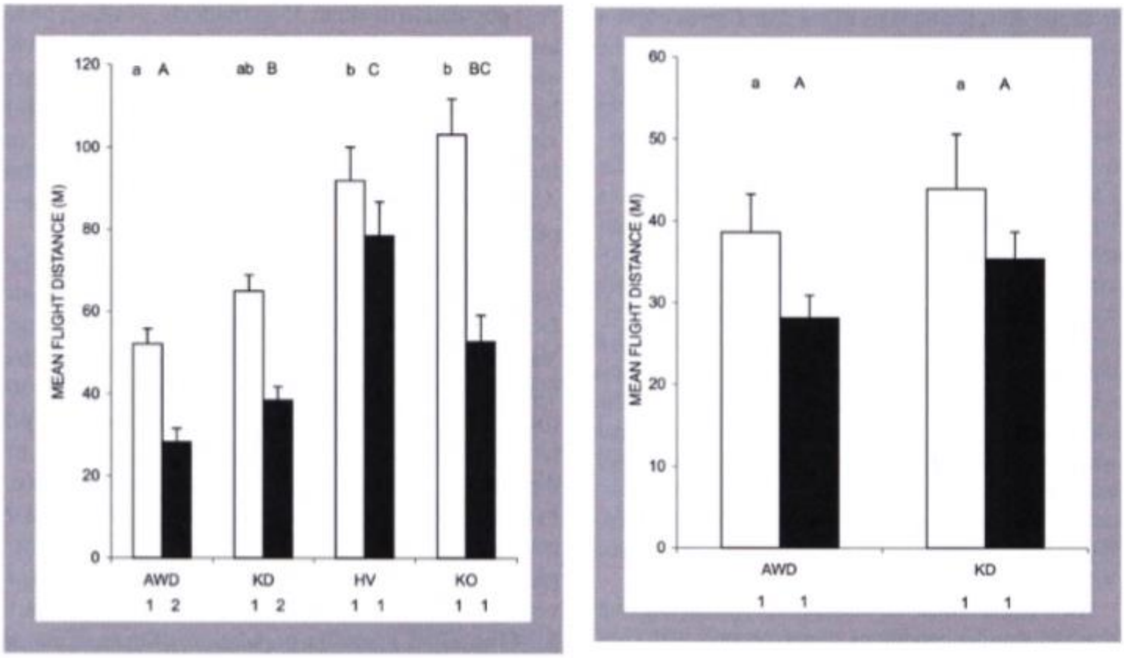


Figure 18: Mean flight initiation distance (Y-axis in meters) of Greenland Caribou across different seasons and groups (X-axis). Adopted from (Aastrup 2000)

18). This after hunting behavior then returned to normal during the summer, when no hunting was present (Aastrup 2000). The study on flight distance in roe deer and fallow deer by de Boer et al. in 2004 shows that hunting leads to increased FID and general wariness in animals. The research was done in four nature reserves in Netherlands, two dune reserves (Amsterdam Water Supply Dunes and Kennemerduinen) and two forest areas (Hoge Veluwe and Kootwijk). The areas are of varied hunting presence gradient from low hunting to high, Amsterdam Water Supply Dunes (AWD) < Kennemerduinen (KD) < Kootwijk (KO) < Hoge Veluwe (HV) (de Boer et al. 2004). Tourism was present in all the areas, with varied number of visitors across the reserves. The terrain also varied, with AWD and KD being rolling dunes and HV and KO were open flat terrain. A total of

291 deer were observed, out of those, 240 were roe deer and 51 fallow deer. The results were that FID of roe deer were significantly shorter in AWD (average of 39 m) then in the other three areas, this is subject to fact, that roe deer are not hunted in AWD. The average FID in KD (50 m) was still shorter then HV and KO (85 m) (Fig. 19a) (de Boer et al. 2004). The fallow deer was present only in two dune areas (AWD and KD). the FID was mostly similar, but it could have been thanks to the low amount of observation of fallow deer in the areas (8 and 4 observations) (Fig. 19b). The study overall confirms that hunting presence increases flight initiation distance and general wariness in animals, as is visible from the (Fig. 19a) where roe deer were hunted much more in HV then in KD. Fallow deer were hardly ever hunted in the two areas of study and their FID stayed mostly the same (de Boer et al. 2004).



a

b

Figure 19a,b: Mean flight distance (Y-axis, in meters) in tested areas (X-axis). Columns represent open (white) and closed (black) vegetation structure. AWD – Amsterdam Water Supply; KD – Kennemerduinen; HV – Hoge Veluwe; KO – Kootwijk. Adopted from (de Boer etl al. 2004)

2.8.3 Animal habituation of non-lethal human disturbance

In general, we can say that the behavior of ungulates in areas with human activity is reflected in the behavior of humans that the animals come in contact with (Geist 1971). Tourism to any given area is causing some changes to how the animals behave when humans are present in their vicinity (Stankowich 2008). Borkowski (2001) did a study on sika deer between 1994 and 1995 in Tanzawa Mountains, Japan. The study area was quite small at 100 ha, but was deemed sufficient, since the radio-collared deer had very little range (between 11.2 and 20.2 ha) and were not moving beyond the area). In the middle of study area, the tourist trail (1.5 km) was present and technically dividing the area in two parts (Borkowski 2001). The amount of tourists vary between seasons, being higher from the late September until June, with rest of the year having less tourism pressure. The

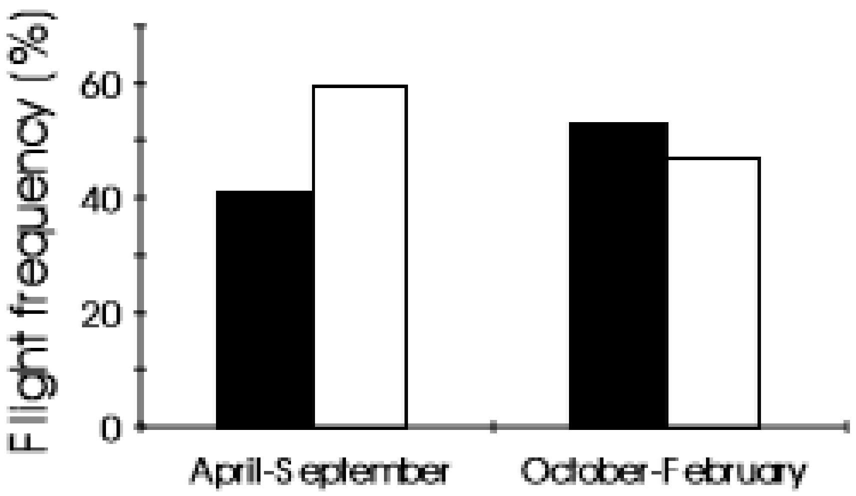


Figure 20: Adopted from (Borkowski 2001)

Figure 21: Adopted from (Borkowski 2001)

tourist trail was walked several days every month four times a day. Number of data were recorded for the walks: number of deer encountered, activity, time, habitat and flight initiation distance with estimates to nearest 5 m. In the end 662 groups of deer were observed. Only 48 % of the groups were caused to take flight, with 52 % not fleeing. Flight frequency was lower between April and September than between October and February (Fig. 20) (Borkowski 2001). The behaviour of the observer played a role in flight frequency, with deer fleeing much more if the observer stopped (Fig. 21). All 69 groups that were less than 10 m from the tourist trail took flight when encountered, but any other incremental distance did not change flight frequency (Borkowski 2001). Sika deer seemed used to human presence, since only about half of the groups fled from the observer, with most of them running no more than 40 m far. Borkowski also observed that in the lower parts of the mountains where hunting antlered sika deer males is allowed, animals were much more wary, then in the higher parts of the mountains where the study took place (Borkowski 2001). Habituation to tourists can also be seen in the study by de Boer et al. (2004) on roe deer and fallow deer, where in Amsterdam Water Supply Dunes visitors can walk freely off-road and roe deer may have gotten used to this behaviour and thus were not that surprised to see the observer approaching them through the vegetation. On the other hand in Kennemerduinen visitors are to stay on the path and animals were more likely to flee at longer distances when present with observer approaching them, this could have in relation of habituation to FID (de Boer et al. 2004).

3. Aims

The aims of the thesis were to review and summarize some of the factors influencing flight initiation distance of animals in the wild and in farm conditions. The other part of the thesis's aims was to discuss results in relation to how we can use FID in farm environment to improve animals' welfare, assess tameness and even preferred treatment of the animals.

4. Methods

I gathered scientific studies and reviews mainly from Web of Science, Science Direct and Wiley Online Library. As a search engine for papers I couldn't find anywhere on sites mentioned above I used Google scholar. The key words that I used were deer, flight, flight distance, behaviour, escape behaviour, deer farms, ungulates, disturbance, tameness and various combinations of them in order to narrow down the number of found scientific material. As I downloaded some of the more vital studies for this thesis, like *Ungulate flight responses to human disturbance: A review and meta-analysis* (Stankowich 2008), and read them, I searched for concrete references mentioned in the study or review. In total I gathered 95 references with 57 used in the thesis. Where possible, I also downloaded citation and created my reference library to make order in my references. I used trial version of EndNote X9 citation manager produced by Clarivate Analytics with corresponding addon for MS Word and using Conservational Biology journal citation style. Where citation was not possible to obtain, I created it by hand. In the end I organized all present results from the studies into one table, containing what kind of factors were studied (e.g. Group size) with corresponding species present in the study and whether they were captive or wild, metric in which the results were measured and where possible the measurment itself and reference to the original study.

5. Results and Discussion

In this chapter the results of the scientific studies and reviews present in this thesis were summarized and discussed. The results were also summarized and organized into one table (Tab. 1).

Table 1: Summarized table of results showing reviewed factors influencing FID with according data of species present in the study, their status as captive or wild, used metric of measurment, where possible,the measurment itself, and reference to the original study (Viktora 2019): FID – Flight initiation distance [m]; ProbFlt – probability of flight [%]; NA – Not available

Factors effects	Species	Status	Metric	Measurement	References
Gentling and treatment					
Not gentled - control - before	Sheep	Captive	FID	4.7 m	Hargreaves & Hutson (1990)
Not gentled - control - after	Sheep	Captive	FID	1.3 m	Hargreaves & Hutson (1990)
Not gentled - sham shorn - before	Sheep	Captive	FID	4.1 m	Hargreaves & Hutson (1990)
Not gentled - sham shorn - after	Sheep	Captive	FID	0.5 m	Hargreaves & Hutson (1990)
Gentled - control - before	Sheep	Captive	FID	2.9 m	Hargreaves & Hutson (1990)
Gentled - control - after	Sheep	Captive	FID	0.7 m	Hargreaves & Hutson (1990)
Gentled - sham shorn - before	Sheep	Captive	FID	2.9 m	Hargreaves & Hutson (1990)
Gentled - sham shorn - after	Sheep	Captive	FID	0.2 m	Hargreaves & Hutson (1990)
Presence of tame animal (TA)					
TA absent	Sika deer	Captive	FID	109 m	Pelikan (2015)
	Red deer	Captive	FID	58.7 m	Pelikan (2015)
	Fallow deer	Captive	FID	144.13 m	Pelikan (2015)
TA present	Sika deer	Captive	FID	14 m	Pelikan (2015)
	Red deer	Captive	FID	30.22 m	Pelikan (2015)
	Fallow deer	Captive	FID	19 m	Pelikan (2015)
Group size					
Large group (>5)	Fallow deer	Wild	ProbFlt	37.10%	Recarte et al. (1998)
	Reindeer	Wild	FID	145.6 m	Aastrup (2000)
Small group (2-5)	Fallow deer	Wild	ProbFlt	41%	Recarte et al. (1998)
Solitary	Fallow deer	Wild	ProbFlt	42.90%	Recarte et al. (1998)
	Reindeer	Wild	FID	93.4 m	Aastrup (2000)
Large groups - larger FID	Guanacos	Wild	FID	NA	Taraborelli et al. (2012)
	Roe deer	Wild	FID	NA	Bonnot et al. (2017)
Large groups - shorter FID	Reindeer	Wild	FID	NA	Reimers et al. (2006)
no effect	Black-tailed deer	Wild	FID	NA	Stankowich & Coss (2005)
	Vicunas	Wild	FID	NA	Donaldio & Buskirk (2006)
	Guanacos	Wild	FID	NA	Donaldio & Buskirk (2006)
	Reindeer	Wild	FID	NA	Colman el al. (2001)
Group composition					
Females > other	Fallow deer	Wild	ProbFlt	NA	Recarte et al. (1998)
	Black-tailed deer	Wild	FID	NA	Coss & Stankowich (2005)
Females w/ young > other	Reindeer	Wild	FID	NA	Colman el al. (2001)
	Sardinian Mouflon	Wild	FID	NA	Ciuti et al. (2008)
Groups w/ young > other	Reindeer	Wild	FID	NA	Aastrup (2000)
No effect of sex	Reindeer	Wild	FID	NA	Reimers et al. (2006)
	Vicunas and Guanacos	Wild	FID	NA	Donaldio & Buskirk (2006)
No effect of age	Reindeer	Wild	FID	NA	Reimers et al. (2006)
	Reindeer	Wild	FID	NA	Colman el al. (2001)
Speed and approach					
Jogging	Black-tailed deer	Wild	FID	88 ± 5 m	Stankowich & Coss (2006)
Walking	Black-tailed deer	Wild	FID	73 ± 6 m	Stankowich & Coss (2006)
Direct approach	Black-tailed deer	Wild	FID	83.4 ± 4 m	Stankowich & Coss (2006)
Indirect approach	Black-tailed deer	Wild	FID	62.5 ± 5 m	Stankowich & Coss (2006)
On foot human disturbances					
High disturbance	Red deer	Wild	Distance from track	avg. 371 m	Sibbald et al. (2011)
Low disturbance	Red deer	Wild	Distance from track	avg. 286 m	Sibbald et al. (2011)
Off-trail > on-trail	Roe deer	Wild	FID	NA	de Boer et al. (2004)
	Fallow deer	Wild	FID	NA	de Boer et al. (2004)
On-trail = off-trail	Roe deer	Wild	FID	NA	de Boer et al. (2004)
On-trail	Sika deer	Wild	ProbFlt	cca 42%	Borkowski (2001)
Off-trail	Sika deer	Wild	ProbFlt	cca 65%	Borkowski (2001)
Continuos walk	Sika deer	Wild	ProbFlt	cca 45%	Borkowski (2001)
Stoping	Sika deer	Wild	ProbFlt	cca 80%	Borkowski (2001)
Hunting					
Areas w/ poaching	Vicunas	Wild	ProbFlt	cca 65%	Donaldio & Buskirk (2006)
	Guanacos	Wild	ProbFlt	cca 70%	Donaldio & Buskirk (2006)
Areas w/o poaching	Vicunas	Wild	ProbFlt	cca 35%	Donaldio & Buskirk (2006)
	Guanacos	Wild	ProbFlt	cca 40%	Donaldio & Buskirk (2006)
Higher FID in areas w/ poaching	Sika deer	Wild	ProbFlt	NA	Borkowski (2001)
	Fallow deer	Wild	FID	NA	de Boer et al. (2004)
After hunting > before	Reindeer	Wild	FID	NA	Aastrup (2000)

5.1 Farm environment – gentling, aversion and their effect on FID

The husbandry practices present in farm conditions have clear influence on how the animals perceive humans, their relationship with them, when they are fearful and when they are relaxed. This subsequently affects their flight initiation distance. The results of the study by Hargreaves & Hutson (1990) showed this, but also proposed that the animals habituate to treatment that is less aversive with enough repetition. Gentling was definitely helping the sheep to habituate to human presence and reducing their flight distance, but this effect was overshadowed by the testing itself just five trials into testing (Hargreaves & Hutson 1990). Farm deer were not tested for FID in the studies present, but the results show that preference for treatment is present in the animals. In study by Pollard et al. (1994) the deer had clear preference of not undergoing the restraint in crush, which is in favour of study by Grigor et al. (1998), where the deer were exposed to five different treatments and restraint was the most aversive one (Pollard et al. 1994; Grigor et al. 1998). If we consider the preference treatment and latency increases of sheep to enter the testing raceway from the Hargreaves & Hutson (1990) study, we could assume that deer would have similar behaviour and that the FID could be dependant on how the animals are treated.

5.2 FID in farm environment

Presence of at least one tame individual among its herd shortened the FID of the whole group considerably. From average fleeing distance of 103.94 meters when no tame animal was present, to 21.07 meters with tame individual present (Pelikan 2015). This could be a considerable advantage in keeping the farm stock approachable by the handlers. The results of the study also presented Red deer as the most approachable on average with no regard to presence of the tame individual with lowest average FID of 44.46 meters. But once we consider the tame deer in the herd, FID shortened significantly more for both other species in the study, Sika deer had average FID of 14 meters and Fallow deer 19 meters versus Red deer with average of 30.22 meters (Pelikan 2015).

5.3 Group size

From the factors that I reviewed, group size seemed to be the most controversial, with no general consensus, with some of the studies showing relation to FID (Recarte et al. 1998; Aastrup 2000; Reimers et al. 2006; Taraborelli et al. 2012) and some not (Colman et al. 2001; Stankowich & Blumstein 2005; Donadio & Buskirk 2006). This may be caused by the fact, that group size may be in fact dependant on other factors, like type of habitat, exposure to humans and history of the population. Therefore, I think that it would be a good factor for further research, preferably in more controlled environment, as the studies present were done on wild populations.

5.4 Group composition

Some studies present in this review showed that sex in group compositions plays a clear role, as females are much more likely to flee sooner than male or even mixed groups, especially if there are offspring present in the female group (Colman et al. 2001; Coss & Stankowich 2005; Ciuti et al. 2008). But as with group size, some studies contradicted that with finding negligible or no evidence of sex or age of the animals in the group influencing FID (Colman et al. 2001; Stankowich & Blumstein 2005; Donadio & Buskirk 2006; Reimers et al. 2006). This factor seemed to be linked to seasonality, as group compositions can change throughout the year and around mating season.

5.5 Speed and approach

The speed and type of approach was clearly influencing FID, as fast and direct movement was clearly seen as a threat. Walking caused animals to flee at average of 73 ± 6 meters, while jogging at the same distance caused animals to flee at longer average range of 88 ± 5 meters (Stankowich & Coss 2007). Direct approach seemed more threatening as animals fled at average of 83.4 ± 4 meters versus 62.5 ± 5 meters when approached indirectly (Stankowich & Coss 2007). This result was understandable, as unexpected stimuli like loud noises and sudden movements are threatening to animals and can easily scare them. Relevant result was from study by Borkowski (2001) where sudden stop while walking caused cca 80% of observed groups of Sika deer to flee (Borkowski 2001).

5.6 On-foot human disturbance

Humans on foot were generally disturbing element for the animals, as they tried to keep away from high disturbance areas. The deer of Mar Lodge Estate area were prime example as they kept their distance from the walking track further back on Sundays, where they were on average 371 meters from the track. Wednesday had on average four times less walkers on the track throughout the day and deer were 286 meters on average far from the walking track (Sibbald et al. 2011). But habituation to humans and their behaviour was visible when the Roe deer were approached by human observer going off-trail in Amsterdam Water Supply Dunes (AWD), where it's allowed and deer are used to it, and when the observer went off-trail and approached the deer in Kennemerduinen, where it is not allowed to wander off-trail, deer reacted much sooner and had larger FID then in AWD (de Boer et al. 2004). This showed that deer were used to certain type of behaviour from humans and unexpected change of behaviour caused them to flee. This same unexpected change of behaviour from humans was present in study on Sika deer of Tanzawa mountains in Japan, where 42% of groups fled while the observer was walking on-trail but climbed to 65% of groups fleeing when the observer went off-trail (Borkowski 2001).

5.7 Hunting

Hunting had always negative impact on FID, as animals in areas with hunting/poaching presence were more wary and fled at larger distances. This was clearly visible when comparing the FID of deer at Amsterdam Water Supply, where Roe deer are not hunted (average FID of 39 meters) and Hoge Veluwe, where roe deer are hunted, with average FID of 85 meters (de Boer et al. 2004). Similar negative impact could be seen in study on groups of Vicunas and Guanacos, which were much more likely to flee when approached in areas where poaching was present, then area where no poaching is present (Donadio & Buskirk 2006).

6. Conclusion

The thesis titled "Flight Initiation Distance – what can tell us about deer farms" summarized present knowledge on some of the factors influencing flight initiation distance. FID at farm conditions can be influenced by how the animals are treated, namely by gentling, non-threatening interaction and even habituation to lesser aversive interaction of the handler and the animal, which positively reinforced the relationship, thus considerably lowering FID. The presence of tame individual among the herd at farm also considerably lowered FID, showing potential in taking advantage of this factor in deer farming. Group size showed that it might not be a factor that directly influences FID and should be more studied, preferably in more controlled environment, like deer farms. Sex and age in group compositions and its influence on FID also seemed to be highly variable across different studies, presenting option that it also might be dependable on other factors, similar to group size. The other types of factors influencing FID showed that unexpected stimuli like sudden movement (or even sudden stop), loud noises and high disturbance areas have negative impact on FID, making the animals more wary of their surroundings, much easier to frighten to the point of fleeing and potentially lowering their fitness.

7. References

Aastrup P. 2000. Responses of West Greenland caribou to the approach of humans on foot. Polar Research **19**:83-90.

Armstrong DM, Fitzgerald, J.P., Meaney, C. A. 2011. Mammals of Colorado. University Press of Colorado, Colorado, US.

Bartoš L 2009. Sika Deer: Biology and Management of Native and Introduced Populations. Springer.

Bartos L, Vankova D, V. Miller K, Siler J 2002. Interspecific Competition between White-Tailed, Fallow, Red, and Roe Deer. The journal of wildlife management. Wiley

Blanco JC, Ballesteros F, García-Serrano A, Herrero J, Nores C, Palomero G. 2011. Behaviour of brown bears killing wild ungulates in the Cantabrian Mountains, Southwestern Europe. European Journal of Wildlife Research **57**:669-673.

Blumstein DT. 2003. Flight-initiation distance in birds is dependent on intruder starting distance. Journal of Wildlife Management **67**:852-857.

Blumstein DT. 2010. Flush early and avoid the rush: a general rule of antipredator behavior? Behavioral Ecology **21**:440-442.

Blumstein DT, Fernandez-Juricic E, Zollner PA, Garity SC. 2005. Inter-specific variation in avian responses to human disturbance. Journal of Applied Ecology **42**:943-953.

Bonnot NC, et al. 2017. Stick or twist: roe deer adjust their flight behaviour to the perceived trade-off between risk and reward. Animal Behaviour **124**:35-46.

Borkowski J 2001. Flight behaviour and observability in human-disturbed sika deer.

Bornett-Gauci HLI, Martin JE, Arney DR. 2006. The welfare of low-volume farm animals during transport and at slaughter: a review of current knowledge and recommendations for future research. Animal Welfare **15**:299-308.

Burton M, Burton, R. 2002. International Wildlife Encyclopedia. Marshall Cavendish, New York, US.

Chapman DI, Chapman, N. G. 1975. Fallow deer: Their history, distribution and biology. Dalton, Lavenham, England.

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*). Behav Processes **77**:408-412.

Colman JE, Jacobsen BW, Reimers E 2001. Summer response distances of Svalbard reindeer (*Rangifer tarandus platyrhynchus*) to provocation by humans on foot. BIOONE.

Cooper W 2005. When and how does starting distance affect flight initiation distance.

Cooper WE, Frederick WG. 2007. Optimal flight initiation distance. Journal of Theoretical Biology **244**:59-67.

Coss RG, Stankowich T. 2005. Effects of predator behavior and proximity on risk assessment by Columbian black-tailed deer. Behavioral Ecology **17**:246-254.

de Boer HY, van Breukelen L, Hootsmans MJM, van Wieren SE. 2004. Flight distance in roe deer *Capreolus capreolus* and fallow deer *Dama dama* as related to hunting and other factors. Wildlife Biology **10**:35-41.

Ditchkoff SS, Lochmiller RL, Masters RE, Hoofer SR, Van Den Bussche RA. 2001. Major-histocompatibility-complex-associated variation in secondary sexual traits of white-tailed deer (*Odocoileus virginianus*): Evidence for good-genes advertisement. Evolution **55**:616-625.

Diverio S, Goddard PJ, Gordon IJ, Elston DA. 1993. The effect of management practices on stress in farmed red deer (*Cervus elaphus*) and its modulation by long-acting neuroleptics: behavioural responses. Applied Animal Behaviour Science **36**:363-376.

Donadio E, Buskirk SW. 2006. Flight behavior in guanacos and vicuñas in areas with and without poaching in western Argentina. Biological Conservation **127**:139-145.

Geist V. 1971. A behavioral approach to the mmanagement of willd ungulates. Pages 413-424. The scientific management of animal and plant communities for conservation. Blackwell Scientific Publications, Oxford.

Geist V 1998. Deer of the World: Their Evolution, Behaviour, and Ecology. Stackpole Books.

Geist VW, F. 1974. The behaviour of ungulates and its relation to managment. Page 936 in Geist V, Walther, F., editor. International Symposium. International Union For Conservation of Nature and Natural Resources, The University of Calgary, Alberta, Canada.

Gilbert C, Ropiquet A, Hassanin A. 2006. Mitochondrial and nuclear phylogenies of Cervidae (Mammalia, Ruminantia): Systematics, morphology, and biogeography. Mol Phylogenet Evol **40**:101-117.

Greig-Smith PW. 1981. Responses to disturbance in relation to flock size in foraging groups of barred ground doves *geopelia striata*. Ibis **123**:103-106.

Grigor PN, Goddard PJ, Littlewood CA. 1998. The relative aversiveness to farmed red deer of transport, physical restraint, human proximity and social isolation. Applied Animal Behaviour Science **56**:255-262.

Guinness THC-BaFE. 1975. Behaviour of red deer (*Cervus elaphus L.*) at calving time.

Hall BK 2005. Bones and Cartilage: Developmental and Evolutionary Skeletal Biology. Elsevier Academic Press, Amsterdam, Netherlands.

Hargreaves AL, Hutson GD. 1990. The effect of gentling on heart rate, flight distance and aversion of sheep to a handling procedure. Applied Animal Behaviour Science **26**:243-252.

Hoffman LC, Wiklund E. 2006. Game and venison - meat for the modern consumer. Meat Sci **74**:197-208.

Kuba J, Landete-Castillejos T, Udała J 2015. Red deer farming: Breeding practice, trends and potential in Poland - A Review. Annals of animal science 2015.

Lehtonen J, Jaatinen K 2016. Safety in numbers: the dilution effect and other drivers of group life in the face of danger. Springer Berlin Heidelberg.

Lidfors L, Jensen P. 1988. Behavior of free-ranging beef-cows and calves. Applied Animal Behaviour Science **20**:237-247.

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

Long CA 2008. The Wild Mammals of Wisconsin. Pensoft, Sofia, Bulgaria.

Long JL 2003. Introduced mammals of the world: their history, distribution and influence. CABI Publishing, Wallingford.

Malo AF, Roldan ERS, Garde J, Soler AJ, Gomendio M. 2005. Antlers honestly advertise sperm production and quality. Proceedings of the Royal Society B-Biological Sciences **272**:149-157.

Metz MC, Emlen DJ, Stahler DR, MacNulty DR, Smith DW, Hebblewhite M. 2018. Predation shapes the evolutionary traits of cervid weapons. Nature Ecology & Evolution **2**:1619-1625.

Nowak RM 1991. Walker's Mammals of the World. John Hopkins University Press, Baltimore.
Pelikan L. 2015. Evaluation of factors influencing flight distance in ungulates. Pages 43. Department of Animal Science and Food Processing. Czech University of Life Sciences, Prague.
Pollard JC, Littlejohn RP, Suttie JM. 1994. Responses of red deer to restraint in a y-maze preference test. Applied Animal Behaviour Science **39**:63-71.
Rácz GR. 2003. Macdonald, D. W., and P. Barrett. 2001. Mammals of Europe. Princeton University Press, Princeton, New Jersey, 312 pp. ISBN 0-691-09160-9, price (paper), $24.95. Journal of Mammalogy **84**:1124-1125.
Ratcliffe P 1987. Distribution and current status of Sika Deer, *Cervus nippon*, in Great Britain.
Reby D, Cargnelutti B, Hewison AJM. 1999. Contexts and possible functions of barking in roe deer. Animal Behaviour **57**:1121-1128.
Reby D, McComb K. 2003. Vocal Communication and Reproduction in Deer. Pages 231-264. Advances in the Study of Behavior. Academic Press.
Recarte JM, Vincent JP, Hewison AJM. 1998. Flight responses of park fallow deer to the human observer. Behavioural Processes **44**:65-72.
Reimers E, L. Miller F, Eftestøl S, E. Colman J, Dahle B 2006. Flight by feral reindeer *Rangifer tarandus tarandus* in response to a directly approaching human on foot or on skis. Wildlife Biology 12.
Rushen J. 1986. Aversion of sheep for handling treatments: Paired-choice studies. Applied Animal Behaviour Science **16**:363-370.
Rushen J, Taylor AA, de Passillé AM. 1999. Domestic animals' fear of humans and its effect on their welfare. Applied Animal Behaviour Science **65**:285-303.
Ruxton GD, Broom M. 2005. You can run—or you can hide: optimal strategies for cryptic prey against pursuit predators. Behavioral Ecology **16**:534-540.
Samia DSM, Blumstein DT. 2014. Phi Index: A New Metric to Test the Flush Early and Avoid the Rush Hypothesis. Plos One **9**.
Samia DSM, Nomura F, Blumstein DT. 2013. Do animals generally flush early and avoid the rush? A meta-analysis. Biology Letters **9**.
Sibbald AM, Hooper RJ, McLeod JE, Gordon IJ. 2011. Responses of red deer (*Cervus elaphus*) to regular disturbance by hill walkers. European Journal of Wildlife Research **57**:817-825.
Stankowich T. 2008. Ungulate flight responses to human disturbance: A review and meta-analysis. Biological Conservation **141**:2159-2173.
Stankowich T, Blumstein DT. 2005. Fear in animals: a meta-analysis and review of risk assessment. Proceedings of the Royal Society B-Biological Sciences **272**:2627-2634.
Stankowich T, Coss R 2006. Effects of predator behavior and proximity on risk assessment by Columbian black-tailed deer. Behavioral Ecology, Volume 17, Issue 2, March/April 2006, Pages 246–254.
Stankowich T, Coss R 2007. Effects of risk assessment, predator behavior, and habitat on escape behavior in Columbian black-tailed deer. Behavioral Ecology, Volume 18, Issue 2, March 2007, Pages 358–367.
Taraborelli P, Gregorio P, Moreno P, Novaro A, Carmanchahi P. 2012. Cooperative vigilance: The guanaco's (*Lama guanicoe*) key antipredator mechanism. Behavioural Processes **91**:82-89.

Williams DM, Samia DSM, Cooper WE, Blumstein DT. 2014. The flush early and avoid the rush hypothesis holds after accounting for spontaneous behavior. Behavioral Ecology **25**:1136-1147.

Williams VM, Pearson, A. B., Jeffrey, G. B., Mackenzie, R.W., Ward, L. J., Fisher, M. W. 2015. A snapshot of New Zealand farmers' awareness of, and self-reported compliance with, animal welfare requirements. Pages 200-204. Proceedings of the New Zealand Society of Animal Production, Dunedin.

Wilson DE, Mittermeier, R.A. 2011. Handbook of the mammals of the world. Hoofed Mammals. Lynx Edicions, Barcelona, Spain.

Ydenberg RC, Dill LM. 1986. The Economics of Fleeing from Predators. Pages 229-249 in Rosenblatt JS, Beer C, Busnel M-C, and Slater PJB, editors. Advances in the Study of Behavior. Academic Press.

Appendices

List of the Appendices:

List of tables:

List of figures: