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Vigilance behaviour of small cervids in South-West Finland: effects of group size, time of day, and predation risk in an agricultural landscape.

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This master's thesis examines the vigilance behaviour of white-tailed deer (*Odocoileus virginianus*) and roe deer (*Capreolus capreolus*) in agricultural landscapes in South-West Finland. The aim of the study was to investigate how potential predator (gray wolf, *Canis lupus*) presence, group size, time of day, and the distance from forest cover affect the vigilance of foraging deer. The main hypotheses were that 1) deer in areas with higher predation risk (wolf presence) were expected to show increased vigilance as an adaptive response to the potential threat posed by predators; 2) vigilance was expected to decrease with increasing group size due to collective detection shared with group members; and 3) deer foraging farther from forest edge were expected to be less vigilant.

The data were primarily collected by using video monitoring during May and June 2024. The influence of wolves was assessed by comparing vigilance-related variables in white-tailed deer observed within core areas of wolf territories (high predation risk/wolf present) and at the edges or outside the illustrated territory boundaries (low predation risk /wolf absent). Interspecific comparisons were conducted only with data from low-risk areas, as roe deer were too rarely observed within high-risk areas to be included in all analyses. During observation bouts, vigilance was measured as 1) the relative proportion of the time an animal was vigilant, 2) the number of vigilance bouts during a fixed observation period, and 3) the average duration of vigilance bouts. The data were analysed using generalized linear mixed models.

The results showed that wolf presence did not increase vigilance in white-tailed deer, as hypothesised. No statistically significant effect was found in foraging distance to nearest forest edge. Instead, group size and time of day were the key predictors: vigilance decreased in larger groups and was highest during twilight hours compared to nighttime. Vigilance frequency was also significantly lower in May than June in white-tailed deer. In the interspecific comparisons, no statistically significant effects were found between the species in any vigilance-related variables. However, in low-risk areas the average vigilance bout duration was influenced by observation month across both species, with bout durations being shorter in June compared to May. These findings suggest that in human-modified landscapes, social and temporal factors may shape the vigilance behaviour of small cervids more than predator presence. Future research should also consider individual-level traits, interspecific competition, and the effects of human disturbance, such as hunting season, on deer vigilance.

Key words: vigilance behaviour, indirect effects of predators, predation risk, ecology of fear

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Tämä pro gradu -tutkielma tarkastelee valkohäntäkauriin (*Odocoileus virginianus*) ja metsäkauriin (*Capreolus capreolus*) valppauskäyttäytymistä Lounais-Suomen maatalousalueilla. Tutkimuksen tavoitteena oli selvittää, kuinka pedon (susi, *Canis lupus*) mahdollinen läsnäolo, ryhmäkoko, vuorokaudenaika sekä etäisyys metsän reunasta vaikuttavat pelloilla laiduntavien kauriseläinten valppauteen. Tutkimuksen keskeisten hypoteesien mukaan 1) kauriiden oletettiin olevan valppaampia alueilla, joilla saalistusriski on suurempi ja suden läsnäolo todennäköisempää, 2) valppauden oletettiin vähenevän ryhmäkoon kasvaessa, koska ryhmän jäsenet jakavat tarkkailuvastuun, ja 3) kauempana metsän reunasta laiduntavien yksilöiden oletettiin olevan vähemmän valppaita.

Aineisto kerättiin pääosin videohavainnoinnin avulla touko-kesäkuussa 2024. Suden epäsuoraa vaikutusta ruokailukäyttäytymiseen arvioitiin vertaamalla valkohäntäkauriiden valppausmuuttujia susireviirien ydinalueilta (korkeampi saalistusriski/susi läsnä) sekä reviirien raja-alueilta tai niiden ulkopuolelta (matalampi saalistusriski/susi ei läsnä). Lajien välistä vertailua tehtiin vain matalan saalistusriskin alueiden havainnoista, sillä metsäkauriita ei havaittu riittävästi susireviirien sisäpuolella kerätyssä tutkimusaineistossa. Valppautta mitattiin tarkkailujaksojen aikana kolmella tavalla: 1) valppausajan suhteellisena osuutena tarkkailuajasta, 2) valppausjaksojen lukumääränä sekä 3) valppausjaksojen keskimääräisenä kestona. Aineisto analysoitiin yleistetyillä lineaarisilla sekamalleilla.

Tulokset osoittivat, ettei suden läsnäolo lisännyt valkohäntäkauriiden valppautta hypoteesin mukaisesti. Myöskään etäisyydellä metsän reunasta ei havaittu tilastollisesti merkitsevää vaikutusta. Sen sijaan lauman ryhmäkoko ja vuorokaudenaika olivat keskeisiä selittäjiä: suuremmissa ryhmissä valppaus väheni ja oli suurimmillaan hämärän aikaan verrattuna yöhön. Valkohäntäkauriin valppausjaksojen määrä oli myös merkitsevästi pienempi toukokuussa kuin kesäkuussa. Lajien välisessä vertailussa matalan saalistusriskin alueilla ei havaittu tilastollisesti merkitseviä eroja lajien valppauskäyttäytymisessä. Havainnointikuukausi vaikutti valppausjaksojen keskimääräiseen kestoon molemmilla lajeilla siten, että jaksot olivat lyhyempiä kesäkuussa kuin toukokuussa. Tulokset viittaavat siihen, että ihmistoiminnan muovaamassa ympäristössä sosiaaliset ja ajalliset tekijät voivat vaikuttaa pienten hirvieläinten valppauskäyttäytymiseen enemmän kuin petojen läsnäolo. Tulevissa tutkimuksissa tulisi tarkastella laajemmin myös yksilötason muuttujia, lajien välistä kilpailua sekä ihmistoiminnan, kuten metsästyskauden, vaikutuksia eläinten valppauteen.

Avainsanat: valppauskäyttäytyminen, petojen epäsuorat vaikutukset, saalistusriski, pelon ekologia

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1 Introduction

1.1 Indirect effects of large carnivores on prey species

Large carnivores are widely recognised for their role in limiting prey populations and influencing ecosystem functioning through both direct and indirect effects on their prey species (Preisser, 2008). Direct regulation occurs through predation, whereas indirect top-down effects influence prey behaviour, physiology, and ecology (Lima & Dill, 1990; Brown, 1999). Through a chain reaction, both direct and indirect effects of top predators on prey species can further affect species on lower trophic levels. This type of chain reaction is referred to as a cascading effect, and can potentially influence broader ecosystem dynamics (Preisser, 2008; Ripple et al., 2014). Such dynamics highlight the significance of predator-prey interactions in shaping and maintaining ecosystem processes and biodiversity.

In the presence of predators, prey species must navigate in environments with varying predation risk while allocating their energy to balance between costs and benefits of deciding when, where, and how to forage, rest, or reproduce. These indirect effects of predators on prey are known as the Ecology of Fear and found in diverse group of species (Brown et al., 1999). According to this concept, prey alter their behaviour to minimise predation risk, even without direct encounters with predators. The fear of predation can therefore create a Landscape of Fear, characterised by spatial variation in predation risk, which depends on the presence and density of predators (Laundré et al., 2001). These fear-driven responses can alter prey species' foraging patterns, habitat use, and reproductive strategies (Lima & Dill, 1990; Zanette & Clinchy, 2025).

If a prey has no evolutionary history with a specific predator, it may not have a response to avoid it either. Prey might also lose their adaptative anti-predator behaviour if a predator is absent for a long period of time, such as hundreds of years (Stankowich & Reimers, 2015). This kind of predation release might affect how prey are able to assess predation risk, and how they are able to escape from a recolonised predator. Small scale adaptation might also occur in certain low predation risk areas, where prey have not experienced any predator encounters in a while (Sirot & Pays, 2011).

Evidence of indirect effects of predators, or predator-induced ecosystem level effects in terrestrial ecosystems, have been primarily found in large conservation areas (Preisser, 2008; Ripple & Beschta, 2012; Gerber et al., 2024). In Europe conservation areas are relatively small and

fragmented, forcing wildlife to adjust to a human modified landscape characterised by agricultural land, deforestation, and habitat degradation. The limited size and isolation of protected areas may constrain the extent to which, for example, cascading effects can spread. This highlights the need for further research on species interactions and community structures under anthropogenic disturbances (Gerber et al., 2024; Kuijper et al., 2024).

1.2 Escape behaviour and vigilance in prey species

The escape behaviour of mammals consists of multiple stages, which vary depending on the presence of a predator and the immediacy of the predation risk (Stankowich & Reimers, 2015). Escaping is always costly, but benefits overcome the costs if the risk of being attacked is acute and the escape is successful. In escape, there is always the possibility of getting injured, which lowers the individual's fitness and its ability to escape the next predator it encounters (Cooper, 2015). However, if prey is killed by a predator, it loses all its fitness, which creates selection for an optimal escape behaviour that balances costs and benefits.

Evolutionary, physiological, social, and environmental factors all influence how prey should evade predator attack, and when it is an optimal time to flee. Before the actual escape, vigilance behaviour is a fundamental strategy, in which prey individuals actively monitor their surroundings to detect potential threats, and prepare for predator encounters (Brown, 1999). Many studies indicate that vigilance behaviour can reduce unnecessary, costly escape attempts (Beauchamp, 2015; Stankowich & Reimers, 2015). Strong evidence also suggests that the more an animal allocates its energy to vigilance, the less likely it is caught by a predator (Lima & Bednekoff, 1999b). Despite the benefits, vigilance can be energetically costly, as the energy allocated to detecting predators may be taken from other important tasks such as foraging or resting (Dimond & Lazarus, 1974; Lima, 1998; Lashley et al., 2014). On the other hand, reducing vigilance is sure to become costly if a predator approaches the prey without it noticing the threat early enough (Lima & Bednekoff, 1999b).

Vigilance of vertebrates has traditionally been measured from the animal's body position and especially from the head-up position (Pulliam, 1973; Beauchamp, 2015). This approach assumes that the animal relies primarily on visual information for anti-predator behaviour. However, especially animals with laterally placed eyes might engage in vigilance even in head-down position, for example while foraging in terrain without visual obstacles (Lima & Bednekoff,

1999a; Fernández-Juricic et al., 2011). In addition to visual monitoring, animals may also increase vigilance in response to acoustic stimuli, underlining the importance of auditory information in escape behaviour (Bhardwaj et al., 2022). Moreover, different patterns of head movement have been linked to responses to varying types of threat (Jones et al., 2007). Vigilance has also been identified to occur either as a routine-like or stimulus-induced behaviour. For example, routine behaviour has been studied by assessing whether a foraging animal continues chewing during vigilance and whether its gaze direction changes during the vigilance bout (Blanchard & Fritz, 2007; McDougall & Ruckstuhl, 2018).

1.2.1 Presence of predators

According to the Landscape of Fear concept, the presence of predators can influence the vigilance levels of prey, as animals must remain alert for potential threats while foraging (Brown, 1999). Building on this, the Risk Allocation Hypothesis suggests that prey species are expected to show behavioural plasticity in response to the spatial and temporal variation in predation risk, increasing their vigilance when the perceived risk is higher (Brown et al., 1999; Lima & Bednekoff, 1999b). Predation risk can vary depending on the season, time of day or predator activity patterns. Moon phases may also influence this risk, as brighter nights during a full moon can enhance visual detection for both prey and predator (Lashley et al., 2014).

1.2.2 Group size effect and alarm signals

For prey species, gathering into groups while foraging can be beneficial for avoiding potential predator attack. In many taxa, studies have found evidence for a group size effect in vigilance behaviour, possibly through a so called Many Eyes Effect (Pulliam, 1973; Lima & Dill, 1990). In larger groups, individuals might rely on collective vigilance among their group members, and therefore reduce their own vigilance (Roberts, 1996; Lashley et al., 2014; Fattorini & Ferretti, 2019). Trusting in shared vigilance frees more time for other tasks, but might also increase the risk of not being able to detect the threat early enough.

Alarm calls and signals play a significant role in vigilance and escape behaviour, both by alerting conspecifics and by influencing predator–prey dynamics (Beauchamp, 2015). For example, McDougall & Ruckstuhl (2018) found that vigilance was more contagious among group members in bighorn sheep (*Ovis canadensis*) if the gaze was fixed and chewing stopped during a vigilance bout. This behaviour was thought to indicate nearby individuals that the vigilance was

triggered by an external stimulus rather than a routine scanning. Similarly, the tail flagging of white-tailed deer has been suggested to be social cue of potential threat to group members (LaGory, 1987).

The evolutionary origins of alarm signals remain debated (Beauchamp, 2015). It is unclear whether such signals primarily evolved to warn conspecifics or to function as pursuit-deterrent signals directed at the predator, indicating that it has been detected and that an attack would therefore be less likely to succeed (Hasson, 1991; Beauchamp, 2015). In this way, prey can assess predation risk for a longer time without escaping immediately. For instance, roe deer (C*apreolus capreolus*) are thought to produce barking sounds (Reby et al., 1999) and white-tailed deer (*Odocoileus* virginianus) use snorting signals (LaGory, 1987) in response to detecting predators. Although these signals are generally low-cost to produce, they can become costly if they draw unwanted attention of a predator and potentially increase predation risk (Beauchamp, 2015). However, when one individual signals, it can elevate vigilance in nearby group members, making collective vigilance more effective under acute threat.

1.2.3 Human influence and disturbance

As mentioned earlier, indirect effects and vigilance behaviour are much less studied under immediate human influence than in more natural settings. Although some animals might benefit from foraging near humans due to artificial food sources and possibly reduced predation risk, studies have also shown humans being able to cause spatial and temporal fear for animals (Sönnichsen et al., 2013; Suraci et al., 2019; Zanette & Clinchy, 2025). Essentially, humans impact large carnivores' habitat selection, hunting behaviour, and activity, which is reflected upon the behaviour of the prey (Oriol-Cotterill et al., 2015; Johnson-Bice et al., 2023). Evidence is also found for prey animals responding to human-posed risk differently compared to risk from natural predators. For example, roe deer have been shown to increase their vigilance levels during the hunting season, as well as in daylight hours, when human hunters were active (Sönnichsen et al., 2013). Also, red deer (*Cervus elaphus*) (Proudman et al., 2020) and elk (*Cervus canadensis*) (Ganz et al., 2024), have been observed to avoid humans during daytime.

1.2.4 Other environmental and ecological factors

Many environmental factors, such as habitat structure and vegetation composition, often interact with predation risk by shaping the behaviour of prey species (Beauchamp, 2015). Also, food

availability and quality play a role in the energy allocation of prey, and how much it can invest in anti-predator behaviour. If food is scarce, animals may have to prioritise foraging over vigilance (Brown, 1999). The influence of foraging distance to cover on vigilance behaviour is debated and many conflicting results have been found across studies (Elgar, 1989). Different flight tactics can also influence habitat choice and therefore vigilance levels under higher predation risk (Lima, 1992; Bonnot et al., 2017; Dellinger et al., 2019). For example, human-made 'easy' terrains, like roads or fields, can influence habitat choice of prey under the Landscape of Fear due to faster possibilities of escape (Johnson-Bice et al., 2023). On an open pasture, deer might be able to detect a predator earlier than in the forest with denser vegetation. Therefore, prey can be found less alert in open areas (LaGory, 1987). In dense vegetation prey species might have better chances of hiding, but also higher chance of losing sight of the predator. Similarly, structural features of habitat, such as edge density, can also shape perceived risk. Recent experimental work found that white-tailed deer showed significantly higher vigilance at high-density habitat edges compared to low-density ones, regardless of whether the patches were connected or isolated (Bartel et al., 2025). This suggests that not only vegetation structure, but also the spatial configuration of habitat boundaries can influence antipredator behaviour.

Additionally, other social factors than group size and alarm signals have been discovered to influence vigilance behaviour. The presence of another species in a group may reduce individual vigilance through shared scanning and improved predator detection, especially when conspecific numbers are low (Fitzgibbon, 1990b; Bartos et al., 2002). However, in larger conspecific groups, vigilance may be neutral or even increase vigilance depending on the specific species interactions (Fitzgibbon, 1990b). Vigilance may also vary among individuals within conspecific groups, depending on group composition. For example, female white-tailed deer have shown increased vigilance in the presence of fawns (Lashley et al., 2014), and when males are present in the same group (Cherry et al., 2015).

1.3 Predator–prey context and the study species

The large carnivore–ungulate system in Southern Finland consists primarily of wolves (*Canis lupus*), Eurasian lynx (*Lynx lynx*), and several cervid species, including e.g. moose (*Alces alces*), roe deer (*Capreolus capreolus*), and the introduced white-tailed deer (*Odocoileus virginianus*). Of these, roe deer and white-tailed deer are the smallest and most abundant cervids in the southern parts of the country, and are important prey for large carnivores. Brown bears

(*Ursus arctos*) and wolverines (*Gulo gulo*) are also native large carnivores, but are rarely observed in South-West Finland (Heikkinen et al., 2024; Mäntyniemi et al., 2025). The red fox (*Vulpes vulpes*) acts as a mesopredator in this system, and may pose a predation risk particularly to fawns of deer species (Jarnemo, 2004).

Historically, wolves have been concentrated in Eastern Finland where they have coexisted primarily with moose and wild forest reindeer (*Rangifer tarandus fennicus*). As a result of conservation efforts, the wolf population has expanded westward into South-West Finland, a region which had previously lacked permanent wolf presence, but has long supported high densities of small cervids. In the 2024 population assessment, wolf territory densities were found to be highest in South-West Finland (Valtonen et al., 2024). In contrast, the Eurasian lynx has maintained relatively stable distribution across Southern Finland (Herrero et al., 2024) and is considered an established predator of small cervids. Although, the consumptive effects of lynx on the cervid populations have not been studied.

1.3.1 White-tailed deer

The white-tailed deer is medium sized (females 60–90 kg and males 90–150 kg) cervid species. It is a non-native species in Finland, but it has a status of game species in the Finnish legislation. It was intentionally introduced from the United States as a new game animal in 1934 and is therefore not classified as an invasive species (Kekkonen et al., 2012). During the first introduction, only four females and one male individual survived the journey from Minnesota to Finland. The animals were initially managed as livestock, but after a tree fell on the enclosure fence and some individuals escaped, the rest were intentionally released into the wild in 1938. After that, new attempts were made to introduce more individuals to Finland to avoid inbreeding among the first four animals, but these attempts were unsuccessful. However, the deer population began to increase gradually, and today the species is widely distributed across Finland, with the highest densities found in South-West Finland. In winter 2023, the population was estimated to be approximately 120 000 individuals (Aikio & Pusenius, 2023).

The home range of white-tailed deer depends on population density, vegetation cover, and food sources, but generally males inhabit larger ranges than females (Poutanen et al., 2022). Females reach maturity around the age of one year and they can have one to three fawns, the earliest in late May and the latest by the first weeks of July. The dispersal of fawns has been studied in their native areas in North America, but limited data exists for Finland. Some studies have

documented dispersal in spring of their first year (Poutanen et al., 2022). White-tailed deer mainly inhabits mixed forests near agricultural areas. It can utilize many types of vegetation in its diet and it frequently forages on a variety of crop species in fields. During winter, it shifts to spruce-dominated forests where snow cover is lighter and it is easier to forage dwarf shrubs, like bilberries. Supplementary feeding of deer by hunters is common in Finland during winter (Poutanen et al., 2023). However, the natural diet of white-tailed deer has not been fully studied in Finland. Increased white-tailed deer numbers have led to a significant rise in traffic accidents, particularly in South-West Finland. Additionally, damage to agriculture and forestry have been increasing rapidly, which has raised economic concerns of the negative impacts of this species (Matala et al., 2021).

1.3.2 Roe deer

The roe deer is a small cervid (20–30kg) native to Finland. It disappeared in the 16th century due overhunting, but was later reintroduced to Åland and Southern Finland in the 20th century. After that, its population started to grow, and finally became established. Nowadays, roe deer carry a legislative status as a game species like white-tailed deer, but there is not as much detailed information available about its density. However, most roe deer sightings have been reported in South-West Finland (Finnish Biodiversity Information Facility, 2025).

The roe deer is a well-adapted species which originally inhabited deciduous forest, but nowadays it mostly occurs in agricultural areas where it effectively utilizes food sources of crop lands, and enjoys the predator release around human settlements (Polameri, 2007). Roe deer also successfully inhabit coniferous forests which can provide cover and more food during winter. Males are highly territorial, especially during summer. The more food is available, the denser a population can be. Females reach maturity at the age of one year and the reproductive capacity remains throughout their life. Roe deer can have one to three, sometimes four, fawns every spring around May or June. Fawns can live with their mother until the next spring.

1.3.3 Wolves in Europe and in Finland

Like other large carnivores worldwide, wolves were driven to regional extinctions across Europe during the 19th and 20th centuries (Chapron et al., 2014; Ripple et al., 2014). Their recovery began when all Europe's large carnivores received a conservation status of strictly protected species in EU's Habitat Directive (Council Directive 92/43/EEC), signed in 1992. Since then,

wolves have been particularly successful in recolonising Europe and adapting into human-dominated landscapes, although they continue to be widely persecuted (Chapron et al., 2014; Kuijper et al., 2024).

Cimatti et al. (2021) identified several drivers facilitating the expansion of large carnivores in Europe, including changes in EU legislation, protected area coverage, reintroduction programmes, and rural land abandonment. Their findings suggest that suitable habitats for large carnivores seem to be areas with increased forest cover and decreased human population. However, they claim that areas with high human densities can also have stable large carnivore populations, if landscape heterogeneity remains high. Due to the recolonisation of wolves, there is a lack of knowledge on the extent of the effects that wolves have on other species and even on entire ecosystems, especially in human dominated landscapes (Gerber et al., 2024; Kuijper et al., 2024).

In Finland, the 19th century trend of declining wolf population was similar to what has been recorded elsewhere in Europe, and the population was nearly hunted to extinction. After the Habitat Directive was signed, the wolf population slowly re-established, but declined again between 2009–2013. Since 2014, the population began to increase once more. In March 2024, the Finnish wolf population was estimated to consist of 277–321 individuals, inhabiting a total of 42 wolf pack territories (Valtonen et al., 2024). All these wolf territories located below the northern Finnish reindeer husbandry area, which covers nearly 36% of Finland's surface area. The Finnish wolf population is divided into eastern and western subpopulation (Mäntyniemi et al., 2022; Valtonen et al., 2024). This has raised a concern of the viability of the western population as it is considerably isolated from other populations, while the eastern population has gene flow through dispersing individuals from the Russian wolf populations.

At the time of conducting this thesis in summer 2024, the hunting of wolves for the purpose of population management was not possible in Finland under either national or EU legislation. However, in March 2025, the legal status of the wolf changed (Council of the EU, 2025). Following a decision by the Standing Committee of the Bern Convention, the wolf was downgraded from Appendix II (strictly protected) to Appendix III (protected). This change was transposed into EU law through Directive 2025/1237, which removed the wolf from Annex IV (Animal and plant species of community interest in need of strict protection) and included it in Annex V (species of community interest whose taking in the wild and exploitation may be subject to management measures) under the Habitats Directive. This legal change allows EU

Member States to apply more flexible population management measures for wolves under Article 14 of the Directive.

Despite the overall protection status and the recent changes to it, the EU's Habitats Directive had already listed wolf populations in Finland's reindeer management area in Annex V. This exception has loosened their protection status within that specific area, allowing the removal of individuals posing a risk to the reindeer industry (Council Directive 92/43/EEC). As a result, large carnivores found in Northern Finland are annually removed with derogation permits.

1.3.4 Predator impacts and knowledge gaps

Vigilance behaviour has been explored in various carnivore–ungulate systems, including wolf–prey interactions, which fall within the scope of this thesis (Laundré et al., 2001; Dellinger et al., 2019; Gerber et al., 2024). However, while both roe deer and white-tailed deer serve as prey for large carnivores in Southern Finland, the quantitative impacts of large carnivores on small cervid populations remain to be investigated in the system, where populations live in a human-dominated landscape and are primarily managed through hunting.

The westward recolonisation of wolf has been linked to the growing white-tailed deer population, which is suggested to be one of the drivers behind the return of wolves to the region (Matala et al., 2021). While wolf research in boreal forests has traditionally focused on larger herbivores, such as moose and wild forest reindeer, evidence from other parts of Europe indicates that smaller cervids also play a role in wolf ecology. For example, research in the Western European Alps demonstrates that high densities of both red deer and roe deer are crucial determinants for wolf habitat selection during their establishment phase (Roder et al., 2020). Although red deer were identified as the most energetically profitable prey, roe deer density also showed a positive association with wolf occurrence. Similar results have been found in study of wolf populations in Sweden and Norway, where roe deer was recognised as the main prey for some wolf packs, and increasing prey density has been linked to wolves maintaining smaller home ranges (Mattisson et al., 2013). Furthermore, due to this recolonisation, wolves represent a relatively new predator for small cervids in South-West Finland, and how deer respond to their presence and predation pressure is still unclear. Understanding how small cervids respond behaviourally to this shift in predator pressure is central to this study.

1.4 Main objectives and research questions

The main aim of my thesis was to examine the vigilance behaviour of both white-tailed deer and roe deer in relation to the presence of grey wolves in South-West Finland, by comparing observations within and outside wolf territories. I hypothesised that deer inhabiting areas with higher predation risk would exhibit increased vigilance as an adaptive response to the potential threat posed by predators (Lima & Bednekoff, 1999b). Since it turned out in the data collection phase that very few roe deer were observed in the wolf territories, the main research question was eventually addressed with data on the white-tailed deer only, while the rest of the analyses were conducted on both species.

In addition to predation risk, I examined how ecological and environmental factors, including group size, distance from the forest edge, and time of day influenced the vigilance behaviour in foraging deer in agricultural fields. I predicted that individuals in larger groups would exhibit lower vigilance frequency and proportion due to collective detection shared among group members (Pulliam, 1973). Additionally, deer further from the forest edge were expected to be less vigilant, as open landscapes enhance visibility, allowing for more efficient threat detection in shorter and fewer vigilance bouts (Elgar, 1989; Lima, 1992; Dellinger et al., 2019).

By addressing these research questions, I aim to enhance understanding on how white-tailed deer adjusts their vigilance behaviour in response to perceived predation risk of wolf and how other environmental factors affect the behaviour of small cervids in a human-dominated landscape.

2 Material and Methods

2.1 Study design

Two types of study areas were selected based on locations of wolf territories, to represent natural variation of predation risk. Four study areas were selected from the core areas of different wolf territories (Figure 1) to represent wolf presence due to the higher predation risk on deer. Five areas were selected outside of the territories, or at the edge of the illustrated territory boundaries (Figure 1) to represent a lower risk of wolf being present in the area. Within each study area, there were one or two fields chosen as study sites, depending on area. All fields had a forest at least on one side of the field edge, and the minimum size of the field was one hectare. The crop on fields was cereals that varied between the sites: the species of cereal was not taken into consideration because no published research is available of what type of crop these cervids prefer the most in Finland.

South-West Finland was selected for this study because this region has the highest white-tailed deer density in Finland (Aikio & Pusenius, 2023) as well as the densest wolf population in Southern Finland (Figure 1; Valtonen et al 2024). Also, roe deer is found very abundant there (Finnish Biodiversity Information Facility, 2025).

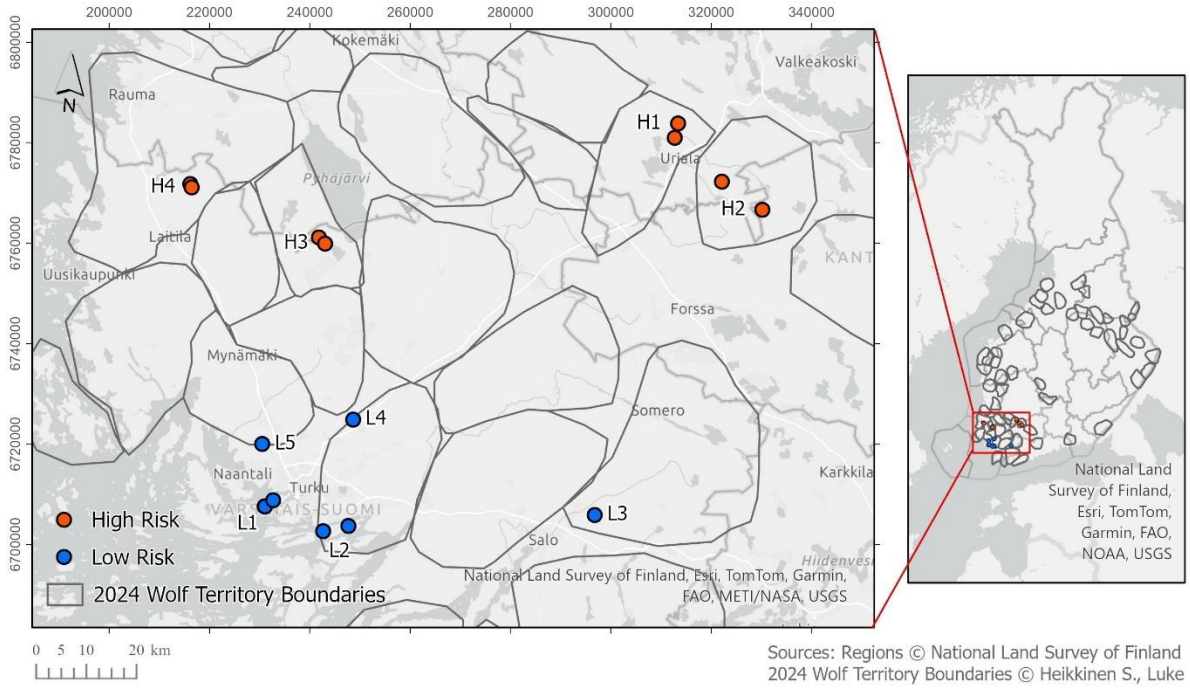

Figure 1. Study site locations in South-West Finland and the illustrated territory boundaries of the wolf population estimated to occur in Finland in March 2024. Areas with high predatory risk of wolf on deer are labelled as H1–

H4 and locations of the study fields within these high-risk areas are marked with red dots. Low-risk study areas are labelled as L1–L5 and the study fields within these are marked with blue dots. High-risk sites are chosen particularly inside of the territories and low-risk sites outside of them or at the edge of the illustrated territory boundary, in order to estimate wolf presence in study area. CRS: ETRS-TM35FIN (EPSG:3067).

Two of the high-risk areas were located in the municipality of Urjala, one in Pöytyä, and one in Laitila (H1, H2, H3, and H4, respectively; Figure 1). In Urjala, area H1 was located within the territory of the Humppila wolf family pack and area H2 inside of the territory of the Toijala family pack (Valtonen et al 2024). Study area H3 in Pöytyä was located within the family pack territory of Vaskijärvi and the territory around H4 belonged to the family pack of Ihode. There were two study fields within each of these territories which in total makes 8 study sites with high predation risk.

The low-risk areas designated as L1, L2, L3, L4, and L5, were located in Turku, Kaarina, Salo, Lieto, and Masku, respectively (Figure 1). More specifically, area L1 in Turku was located on Ruissalo Island and area L2 in Kaarina on Kuusisto Island. A total of seven study fields were chosen across these low-risk areas, with L1 and L2 containing two fields each, and L3, L4, and L5 containing one field each.

As shown in Figure 1, a significant number of wolf territories occur relatively near each other in South-West Finland. Due to this high wolf density, identifying control areas entirely free from wolf activity was challenging. Therefore, in low-risk areas, the possibility that some wolves may have passed through the area or that the observed ungulates might have had previous encounters with wolves at some point in their life, must be acknowledged. Overall, low-risk areas represent areas without significant wolf presence and the high-risk areas assume continuous wolf presence in the territory.

Other predators, like red fox and Eurasian lynx, were most likely present in both high-risk and low-risk areas during the study period. In this thesis the fear effects of other possible predators are assumed to be constant regardless of the presence of wolf, because there were no tools to exclude or measure their densities. However, according to the 2024 lynx population assessment (Herrero et al., 2024), lynx were distributed relatively evenly across South-West Finland, supporting the assumption of consistent lynx presence in the study area.

2.2 Research equipment

Data was collected by i) detecting animals from a car with binoculars, ii) observing the animals on forest edges via telescope and by taking video recordings of the animals with a phone adapter, and iii) by using two types of surveillance cameras.

All study areas with a camera setup had to have landowners' permission which limited the locations of study areas. The camera equipment consisted of four Reolink wildlife cameras (Go Ranger PT) and nine surveillance cameras (SD49225XA-HNR-P Dahua PTZ Lite-AI IR 2 Mpx 25x, 4.8–120 mm). Ruissalo island was the only study site where observations were collected only manually by using binoculars and telescope (Figure 2 a), but all the other study fields had one set of camera equipment each (Figure 2 b, c). The majority of the observations were collected with the surveillance cameras.

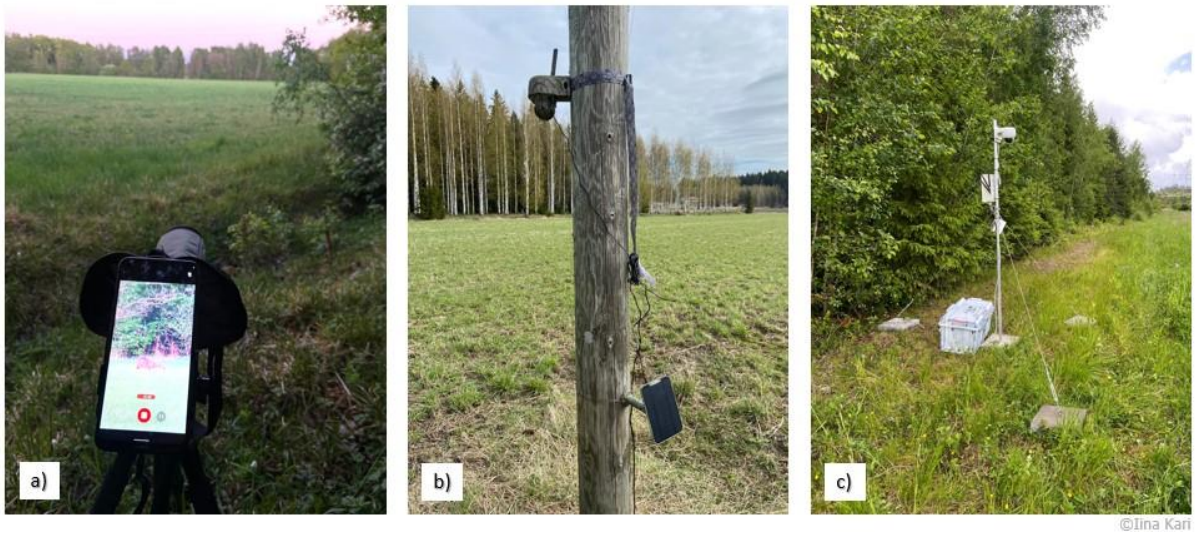

Figure 2. Alongside 10x42 binoculars, the research equipment consisted from a) a telescope with phone adapter, b) Reolink trail cameras with solar panel, and c) surveillance cameras attached to metal pole with external battery.

Solar-powered, 355°-rotating Reolink cameras (Figure 2 b) were used exclusively on study areas H1 and H2 in Urjala. Reolinks were set to detect animal movement at nighttime from 8 p.m. to 7 a.m. From each movement detection the video turned on and kept recording for 30 seconds. This meant that some records lasted only 30 seconds and some several minutes. Reolink cameras accessed internet via a SIM-card so it was possible to remotely turn the camera frame through the Reolink -application 24/7. Video recordings were saved on 128GB SD-cards.

Other surveillance camera setups (Figure 2 c) were made for ecological research purpose by Airaksinen et al. (2024) when they conducted research of damage to fisheries caused by cormorants (*Phalacrocorax carbo*) and grey herons (*Ardea cinerea*). In the setup, cameras were placed on 2-meter-tall metal poles with three metal wires attached on concrete tiles which kept the camera pole steady even in harsh weather conditions. In this study one set of camera equipment was placed on the side of each study field on areas H3–H4 and L2–L5. Cameras had an external battery (Tab HD 12V 100Ah LiFePO4 BT) which had to be changed about once a week. Each camera was equipped with an IP-protected industrial cellular router (RUT240/RUT241), which could access the internet via SIM-cards. Cameras rotated 365° and could be remotely controlled from Dahua Config Tool. These surveillance cameras recorded non-stop video material between a set time frame, from 8 p.m. to 7 a.m. Material was sent in 60-minute video clips from the router to the FTP server every hour throughout the night. The recordings could be downloaded into an external data storage drive from the FTP server by using the FileZilla application.

2.3 Data collection

Data was collected by using the focal animal sampling method (Altmann, 1974) with a ca. five-minute observation time. Only adult individuals were selected as samples and every observation bout that lasted a minimum of two minutes were included in the data set.

At study sites, where data were collected by camera equipment, each animal visible in the video frame was selected as soon as it started to forage. If there were many deer present, individuals were chosen so that all group members were observed within the same time slot. However, in Ruissalo, where data were collected on-site, focal animals were selected randomly, either the first animal detected or the one most easily visible. When all group members were clearly visible, observations proceeded systematically (e.g., from left to right) to ensure each individual was recorded once. The wind direction and distance between observer and the animals was considered, to avoid disturbing the foraging deer. Additionally, ten minutes were waited on site before the start of the first observation bout, to make sure that the deer were not paying attention to the observer.

In this study, vigilance behaviour was used as an indicator of possible indirect fear effects caused by wolf presence (Blanchard & Fritz, 2007; Sönnichsen et al., 2013; McDougall & Ruckstuhl, 2018). A detected animal was recorded as ‘vigilant’ if its head was above shoulder

level (Figure 3 c), and ‘not vigilant’ if the head was at the shoulder level or below that (Figure a, b) (Fitzgibbon, 1990a). The total vigilance duration during observation bout was timed and the frequency of head-up positions were counted.

When deer search food or move around while foraging, the head is usually at shoulder level (Figure 3 b). During these search walks, an animal was counted as ‘not vigilant’. Also, if the animal was feeding in long vegetation or if it scratched its back (head being above shoulder level), the behaviour was counted as ‘not vigilant’. If the animal laid down during the observation bout, it was counted as ‘not vigilant’ because most of the time the vegetation was too tall to tell whether the behaviour of laying deer was calm or vigilant.

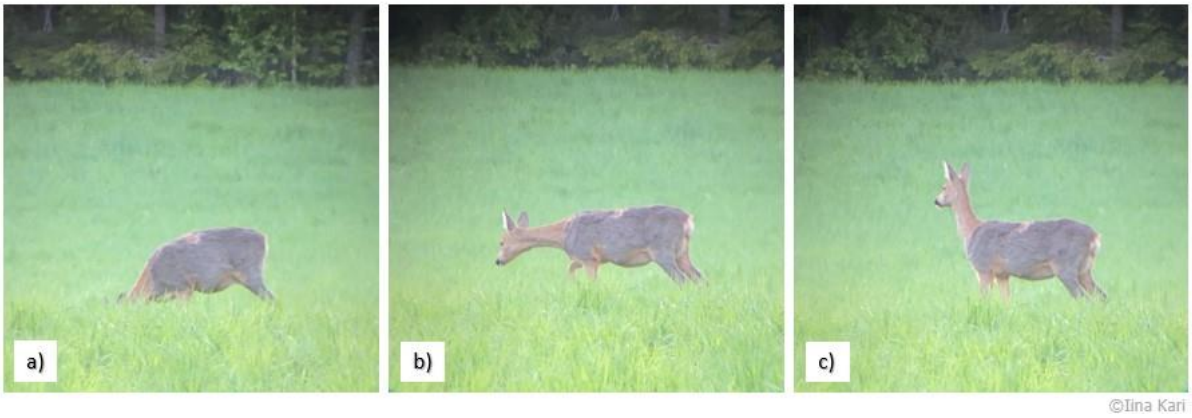

Figure 3 Most common head positions of foraging deer during observation bout. Head-down events can be seen in pictures a and b. Picture a) shows the foraging position where the head is clearly down below the shoulder level. When a deer searched a new food patch, its head was usually in a neutral, horizontal position (b), and this behaviour was counted as ‘not vigilant’, as well as the foraging position. Animal was counted as ‘vigilant’ if the head was above the shoulder level (c). These pictures of roe deer are taken with phone attached to the telescope.

All observation bouts were timed with the Stopwatch+ application on an iPhone, with records exported directly via email to prevent typing errors. The observation bouts began when the deer was in the foraging position, so the first lap on stopwatch marked the start of the first vigilance bout. Timing ended after five minutes, unless interrupted by events such as the animal leaving view, video cuts, or human disturbance. In cases when the animal’s head was in an upward position at the five-minute timestamp, recording was continued until the head was returned down in the foraging position. All video material where humans were detected was removed, and no vehicles were detected in any recordings.

The group size was defined as the number of deer visible in the beginning of the observation bout in the same field or video frame. It was recorded at the start because some group members

might have been laying down when observations began or could have left the field or video frame during the observation bout. The distance of the focal animal to the nearest forest edge was also recorded in the beginning of each observation bout, since deer were usually moving while foraging. The distance from the nearest forest edge was a categorised estimate, based on the known diameter of the study field and the estimated standing location of the focal animal. Distance from the forest edge was divided into three categories (1 = <20 m, 2 = 20–50 m, 3 = >50 m).

Data were collected between 9th of May and 20th of June 2024. For analysis, the collection time of each observation bout was categorised as follows; sunset (8 p.m.–12 a.m.), night (1 a.m.–4 a.m.), and sunset (5 a.m.–9 a.m.). All cameras had a night vision feature, which worked well as the nights did not get too dark in midsummer due to the unique light conditions at Finland's latitudes. Additionally, I requested and was granted data of weather conditions from Natural Resources Institute Finland; however these data were not included in the final models.

2.3.1 Identifying study species

Study species were identified from the video records by recognising their species-specific characteristics. White-tailed deer are larger than roe deer and they have a longer tail which is white underneath and dark brown on top (Figure 4). In contrast, roe deer are smaller and their tail is almost invisible, but instead they have a white rump patch which is recognisable especially when they are fleeing (Figure 5). Roe deer also have rounder face than white-tailed deer. If the focal animal was far away, the body size and possible the tail flagging of white-tailed deer usually helped in identifying the species from each other.

Figure 4 Two white-tailed deer captured with Reolink -trail camera.

Figure 5 Two roe deer recorded with surveillance camera.

Individual's sex on the other hand was usually hard to determine as the pixels on surveillance cameras faded the thin antlers in certain frame angles, especially on nighttime records. In unsure cases, whether the animal had antlers or not, the sex was not specified. This explains why sample size of confirmed sex differs from the total sample size. Therefore, sex was not included in any of the models.

3 Statistical Analysis

3.1 Dataset

The final dataset contained 83 observations from low-risk areas and 107 observations from high-risk areas (Table 1). The low-risk dataset included 62 roe deer and 21 white-tailed deer observations, whereas in high-risk areas only three roe deer observations were recorded, compared to 104 white-tailed deer observations. Due to this imbalance, the effects of wolf presence could not be analysed for roe deer across different predation risk contexts. Therefore, the first analysis focused solely on white-tailed deer, using data from both risk areas to assess the effects of wolf presence on vigilance behaviour. Additionally, to examine whether group size differed between the two risk areas of wolf presence, a Wilcoxon rank-sum test was conducted.

Table 1 Number of species recorded from each study area during the study period.

Study Area	Roe Deer	White-Tailed Deer
Low-risk		
L1	40	0
L2	17	13
L3	0	3
L4	0	5
L5	5	0
High-risk		
H1	0	32
H2	0	14
H3	2	15
H4	1	43

The second set of analyses examined interspecific differences in vigilance behaviour under shared ecological and temporal conditions. These comparisons included only observations from low-risk areas. Wilcoxon rank-sum test was run to find group size differences between the species observations.

3.2 Data exploration and descriptive statistics

The distributions of all vigilance-related variables (proportion, frequency and duration) were checked for normality, both graphically and statistically. Since the original observation time varied, the counted vigilance frequency divided with observation time (s) and multiplied by 60, to calculate average vigilance frequency per minute for each observation. Levene's -test was

applied to test for homogeneity of variances prior to conducting parametric tests. All outlier individuals were cross-checked against field notes to ensure that no external disturbances (e.g., sudden human activity) had influenced the recorded behaviour.

For both the species-specific analysis of white-tailed deer and the interspecific comparison with roe deer, the same set of descriptive statistics, including mean, variance (Var), standard deviation (SD), and standard error (SE), were calculated for all vigilance-related variables. Variance and SD quantify the degree of individual behavioural variability within each group, while SE reflects the reliability of the sample mean estimates.

For white-tailed deer, observation bout durations ranged from 2 minutes to 7 minutes and 25 seconds, with a mean duration of 4 minutes and 68 seconds. Descriptive statistics were calculated separately for all vigilance-related variables in high-risk (wolf present) and low-risk (wolf absent) areas. Lower SE values suggest more precise estimates and are important for interpreting differences between risk areas. As the analysis aims to compare vigilance behaviour in different predation risk contexts, these statistics provide a baseline for assessing whether observed differences in the model outputs are likely to reflect true biological patterns or sampling uncertainty. For the interspecific comparison, roe deer and white-tailed deer were analysed in absence of wolf (low risk areas). Observation durations ranged from 2 to 8 minutes with average of 4 minutes and 59 seconds in low-risk areas. The same descriptive statistics were computed for both species, allowing a direct comparison of vigilance behaviour under shared ecological conditions.

3.2 Modelling

Generalized linear mixed models (GLMM) were fitted for vigilance proportion, frequency, and average vigilance bout duration using two datasets: one with white-tailed deer observations from both risk areas, and another including both species but limited to low-risk areas only. Each model included one vigilance-related response variable: 1) vigilance proportion (the proportion of time an animal was observed having head raised above shoulder level relative to the total duration of the observation bout), 2) vigilance frequency per minute (the number of vigilance bouts during the observation bout divided by observation time), or 3) average vigilance bout duration (calculated as vigilance proportion divided by total vigilance frequency during the observation bout). Vigilance frequency per minute was log-transformed for white-tailed deer models, using the natural logarithm (log(x)) to reduce right skewness in the data (Salinas Ruíz

et al., 2023). This transformation improved the distributional properties of this response variable, allowing the use of a gaussian distribution in the model. For interspecific model on vigilance frequency, the logarithmic transformation was not needed as data was normally distributed on low-risk areas. This analysis was only done in low-risk area due to lack of data in high-risk area.

Study field (nested within study area) and the group ID-number were entered as random effects, to account for the non-independent observations within specific areas, and group-level dependencies as individuals within the same group might share common influence between the group members. Wolf presence in the study area (low risk, high risk) was a fixed effect in the models for white-tailed deer. Group size, observation month (May, June), and categorial variables such as time of day (sunset, nigh, sunrise), and the distance from the forest edge (<20 m, 20–50 m, >50 m) were included as fixed explanatory variables, depending on model. Data from low-risk areas included only two observations of furthest forest distance category (>50 m). Those observations were pooled with the intermediate distance category (20–50 m) in interspecific modelling, to avoid problems in model fitting. Similarly, roe deer observations included only a few sunrise observations, which were subsequently pooled with night observations.

Modelling was conducted with the RStudio (4.1.2) glmmTMB-package (v. 1.1.7, Brooks et al., 2017), in which hierarchical nesting of dependent variables was possible. A backwards selection approach was used in choosing the best model fits (Zuur et al., 2007). In this approach, all variables were included in the first model. Then, covariates were reduced one at time, until the lowest AIC-value was found.

4 Results

4.1. Vigilance behaviour of white-tailed deer in the presence of wolf

Descriptive statistics of white-tailed deer show higher variation in all measured behavioural variables in high-risk areas (Table 2). However, the number of observations in high-risk areas were 79,81% higher compared to number of observations collected from low-risk areas. The total number of observations (N) of white-tailed deer was 125. However, some observations on low-risk areas lacked data on some variables, so sample size (n) in all of the following models were 120.

Table 2 Descriptive statistics for white-tailed deer behaviour in low predation risk and high predation risk areas. N = Sample size, VAR = variance, SD = standard deviation, SE = standard error.

Behaviour Variable	Risk Area	N	Min	Max	Mean	Var	SD	SE
Vigilance Proportion (%)								
	Low-risk	21	7.8	47.9	25.7	154.0	12.4	2.7
	High-risk	104	<0.1	92.9	22.0	366.0	19.1	1.9
Vigilance Frequency per minute								
	Low-risk	21	1.3	5.0	2.6	0.7	0.9	0.2
	High-risk	104	0.2	6.5	2.1	1.7	1.3	0.1
Average Vigilance Bout Duration (s)								
	Low-risk	21	3.0	16.0	6.8	12.1	3.5	0.8
	High-risk	104	1.0	68.0	8.7	128.0	11.3	1.1

The Wilcoxon rank-sum test did not reveal a statistically significant difference ($W = 864$, $p = 0.111$) in group sizes between risk areas, which indicates that the group size was relatively consistent across the study sites and unlikely to influence the vigilance models (Figure 6).

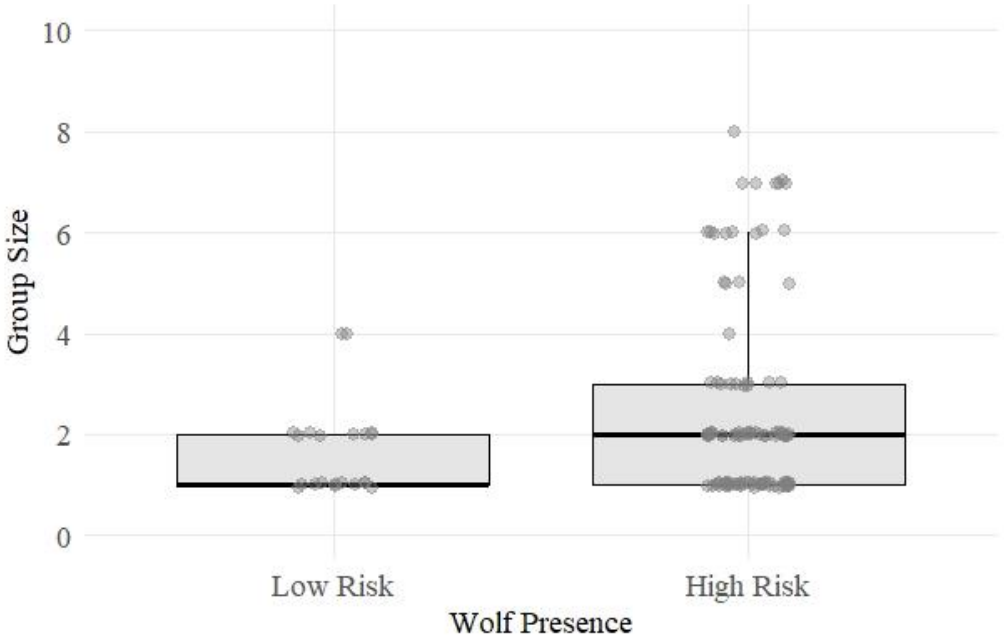

Figure 6 The group sizes in which each white-tailed deer was observed in low-risk (n = 21, mean ± SD = 1.67 ± 0.91) and high-risk areas (n = 104, mean ± SD = 2.48 ± 1.93). Solitary individuals were recorded as group size one. The boxplots illustrate the distribution of group sizes: the horizontal line marks the median, the boxes represent the interquartile range, and the whiskers extend to the extreme non-outlier values (no whisker is shown for the low-risk area due to the narrow data range). Individual observations are overlaid as dots, with points beyond the whiskers representing outliers.

4.1.1 Vigilance proportion

The proportion of time white-tailed deer spent vigilant while foraging, modelled using a beta distribution with a logit link (Salinas Ruíz et al., 2023), was significantly influenced by group size and time of day, but not by predation risk or distance from the forest edge (Table 3). Among the random effects, individual group-level differences contributed more to variation in vigilance proportion than spatial factors. The model included 120 observations after excluding incomplete records on predictor data. The sample size divided between risk areas so that 104 observations were from high-risk areas and 16 from low-risk areas. The predicted vigilance proportion was 23.88% [95% CI: 15.03, 35.75] in low-risk areas and 21.40% [95% CI: 16.49, 27.26] in high-risk areas.

Group size had a significant negative effect on vigilance proportion (Table 3). As shown in Figure 7, the proportion of time deer spent vigilant declined with increasing group size. Model predicted the group size declining approximately 14% with each group member. Time of day also significantly affected vigilance ($p < 0.05$; Table 3). Vigilance was lowest during the night, compared to sunset and sunrise (Table 4 a). Pairwise comparisons showed that these differences

were statistically significant (Table 4 b). Vigilance levels at sunset and sunrise did not differ significantly ($p > 0.05$; Table 4 b), suggesting similar levels of alertness during twilight hours. Predicted values for vigilance proportion on different time categories are visualised in Figure 8.

Table 3 Fixed and random effects from beta regression GLM model explaining vigilance proportion in white-tailed deer. Table includes chi-square test values, degrees of freedom, p-values, and coefficient estimate for wolf presence, group size, distance from forest edge, and time of day. Type III Wald chi-square tests were used to assess the significance of fixed effects which included wolf presence, group size, distance to forest and time of day. Group size and time of day appeared as statistically significant explanatory variables ($p < 0.05$).

Vigilance Proportion	Wald χ^2	Df	p-value	Estimate	SE
Fixed factors					
Intercept	7.87	1	0.005	-0.79	0.28
Wolf Presence (high risk, low risk)	0.29	1	0.587	0.14	0.26
Group Size	4.21	1	**0.040**	-0.15	0.07
Distance to Forest (<20 m, 20–50 m, >50 m)	0.38	2	0.826	-	-
Time of Day (sunset, night, sunrise)	7.46	2	**0.024**	-	-

Random effects	Variance	Std. Dev.
Study Area	<0.01	<0.01
Field (nested within study areas)	<0.01	<0.01
Group ID	0.21	0.45

Model fitted with beta distribution (logit link). Estimates are calculated with low risk as the reference category in the wolf presence.

Table 4 Time of day effects on vigilance proportion with pairwise comparisons. (a) presents estimated marginal means, standard errors, 95% confidence intervals, and (b) Tukey-adjusted p-values comparing vigilance proportions between sunset, night, and sunrise.

Time of Day	Estimated model mean	SE	95% CI
a)			
Sunset (8 p.m.–12 a.m.)	-1.146	0.17	[-1.49, -0.81]
Night (1 a.m.–4 a.m.)	-1.689	0.30	[-2.21, -1.17]
Sunrise (4 a.m.–9 a.m.)	-0.857	0.33	[-1.50, -0.22]

b) Comparison	Estimate (log odds)	SE	z-ratio	p-value
Sunset–night	0.543	0.23	2.371	**0.047**
Sunset–sunrise	-0.290	0.31	-0.937	0.617
Night–sunrise	-0.832	0.35	-2.362	**0.048**

Results averaged over Distance from Forest and Wolf Presence. Tukey-adjusted p-values. Estimates given on the logit scale.

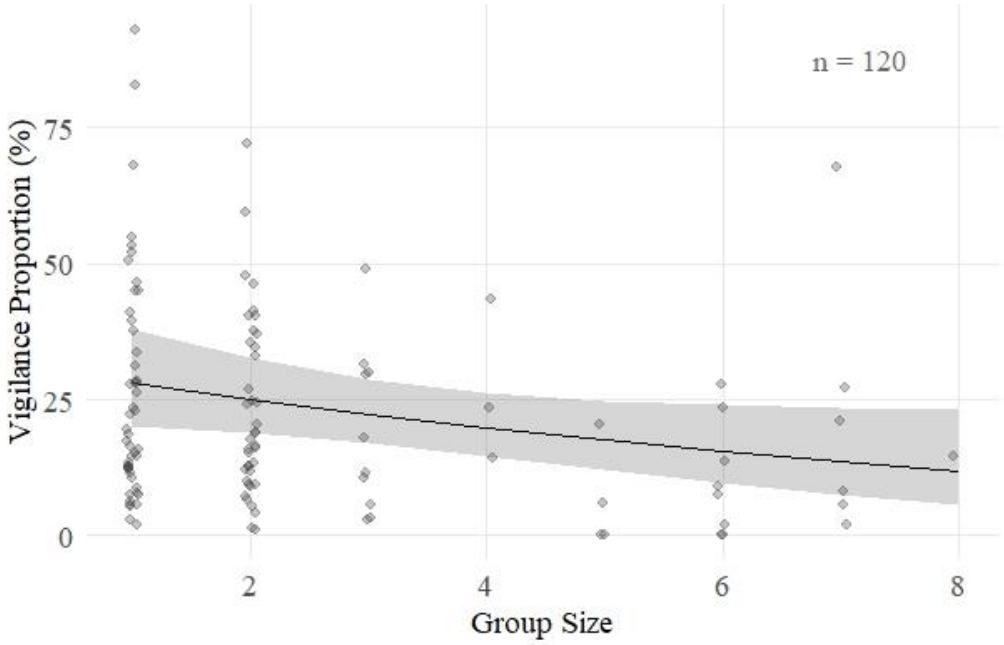

Figure 7 Effect of group size on the proportion of time white-tailed deer spent vigilant. Each point represents one observation bout of ca. 5 minutes. To improve visualization of overlapping data points, a small amount of random jitter was applied to the x-axis positions. The solid line shows modelled predictions with 95% confidence intervals, based on a beta regression model. All modelled values are backtransformed on the original (proportion) scale.

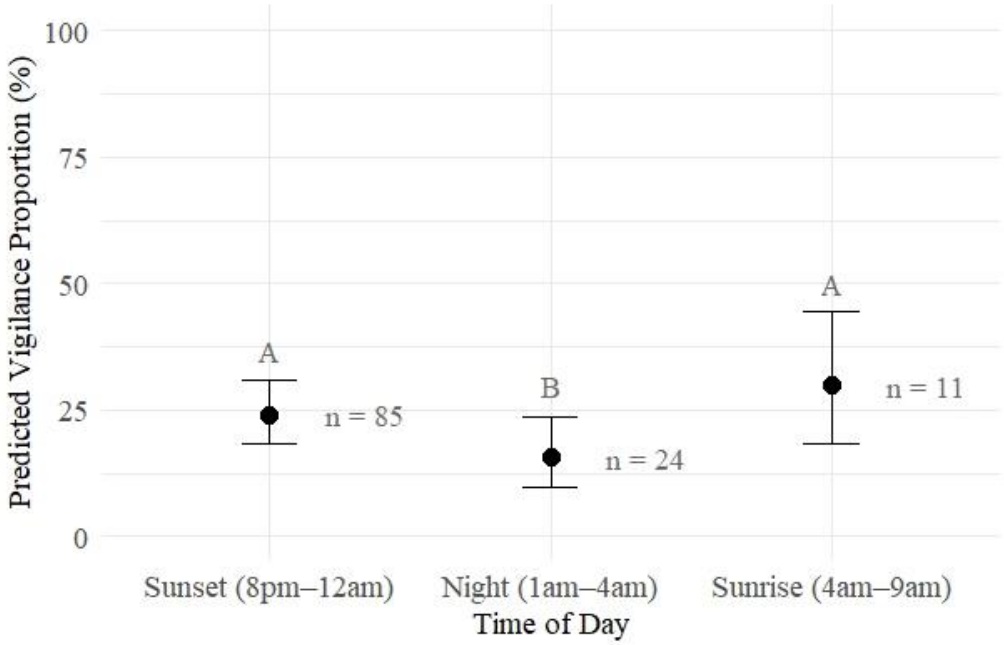

Figure 8 Predicted proportion of time white-tailed deer spends vigilant at different times of day. Modelled means and 95% confidence intervals are shown on the backtransformed scale. Sample size (n) shows how data is distributed across categories. Vigilance was lowest during the night compared to twilight periods. Letters above the confidence intervals indicate statistically significant groupings, showing that sunset and sunrise (A) did not differ significantly from each other ($p > 0.05$), while night (B) differed significantly from both ($p < 0.05$).

4.1.2 Vigilance frequency

Vigilance frequency per minute (log-transformed) was analysed using gaussian distribution in GLM model (Salinas Ruíz et al., 2023). Vigilance frequency in white-tailed deer was significantly affected by group size, time of day, and observation month (Table 5). A marginal difference indicated vigilance frequency being lower in high-risk areas compared to low-risk areas, but the difference did not reach statistical significance ($p > 0.05$; Table 5). Predicted vigilance frequency was 2.5/minute [95% CI: 1.62, 3.74] in low-risk areas and 1.6/minute [95% CI: 1.21, 2.04] in high-risk areas. Group size had a significant negative effect on vigilance frequency with fewer vigilance bouts observed in larger groups (Table 5). According to the model, each additional group member was associated with an approximately 8% decrease in vigilance frequency. The modelled decline on vigilance frequency is presented in Figure 9.

Time of day also significantly influenced vigilance frequency ($p < 0.05$; Table 5). The frequency was lowest at nighttime and higher both during sunset and sunrise (Table 6 a). However, pairwise comparisons revealed that the differences were marginally non-significant between the time categories, in which sunset compared to night, and night compared to sunset differed more from each other, while vigilance frequency was quite similar between twilight hours (Table 6 b). Results are shown in Figure 10 with original scale of the count data adjusted per minute. There was also a significant ($p < 0.05$; Table 5) effect of month on vigilance frequency, in which the frequency was higher in June compared to May, as presented in Figure 11 with backtransformed values. Study field explained a very small amount of variance among the random effects, while Study area and Group ID contributed none. Residual variance represents the amount of variation that is left unexplained by fixed and random effects.

Table 5 Fixed and random effects from a generalized linear mixed model (GLMM) explaining vigilance frequency per minute in white-tailed deer. The response variable was log-transformed to improve normality and meet model assumptions, as the original frequency data were positively skewed. Fixed effects included group size, wolf presence, forest distance, time of day, and observation month. Random effects included study area, nested study field, group size, and residuals representing variation which is not explained by fixed or random effects. Model was based on 120 observations (high-risk, 104; low-risk, 16).

Vigilance Frequency (/min)	Wald χ^2	Df	p-value	Estimate	SE
Fixed factors					
Intercept	5.68	1	0.017	0.53	0.22
Wolf Presence (high risk, low risk)	3.66	1	0.056	0.45	0.23
Group Size	4.64	1	**0.031**	-0.08	0.04
Distance from Forest (<20 m, 20–50 m, >50 m)	1.13	2	0.567	-	-
Time of Day (sunset, night, sunrise)	7.43	2	**0.024**	-	-
Observation Month (May, June)	4.86	1	**0.027**	0.41	0.19

Random effects	Variance	Std. Dev.
Study Area	<0.01	<0.01
Field (nested within study areas)	0.04	0.20
Group ID	<0.01	<0.01
Residual	0.31	0.56

Model fitted with gaussian distribution (identity link). Estimates are presented on the log scale, and are calculated with low risk as the reference category in the wolf presence and June in observation month.

Table 6 Model means and pairwise comparisons of log-transformed vigilance frequency across time of day categories (sunset, night, sunrise). Vigilance was highest at sunrise and lowest at nighttime. None of the pairwise comparisons reached statistical significance ($p > 0.05$), although two comparisons approached significance with marginally higher vigilance frequency at sunset compared to night, and marginally lower frequency at night compared to sunrise.

Time of Day	Estimated model mean	SE	95% CI
a)			
Sunset (8 p.m.–12 a.m.)	0.747	0.11	[0.52, 0.97]
Night (1 a.m.–4 a.m.)	0.399	0.17	[0.06, 0.73]
Sunrise (4 a.m.–9 a.m.)	0.879	0.21	[0.46, 1.30]

b) Comparison	Estimate (log odds)	SE	t-ratio	p-value
Sunset–night	0.348	0.15	2.337	0.055
Sunset–sunrise	-0.132	0.19	-0.690	0.770
Night–sunrise	-0.480	0.21	-2.318	0.058

Results averaged over Wolf Presence, Distance from Forest, and Observation Month. Tukey-adjusted p-values. Estimates are given on log scale.

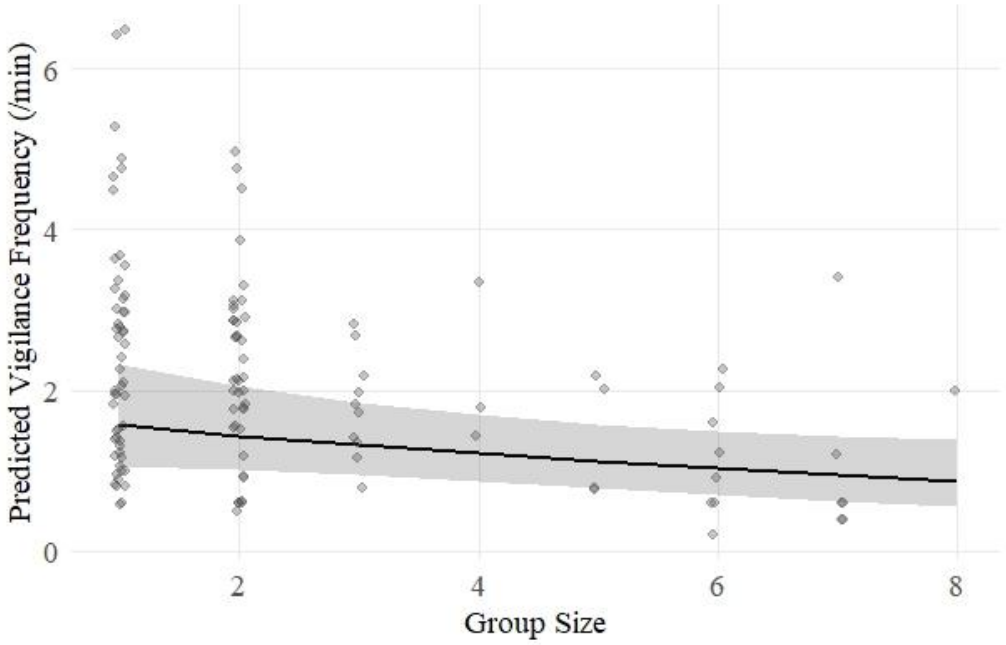

Figure 9 Modelled relationship between group size and vigilance frequency (/min) in white-tailed deer. Dots represent frequency values adjusted to observation bouts (n = 120), with slight x-axis jitter applied to reduce overlap. The curve and shaded area represent modelled predictions and 95% confidence intervals from a gaussian model, presented on the backtransformed scale. According to the model, vigilance frequency decreases when group size increases.

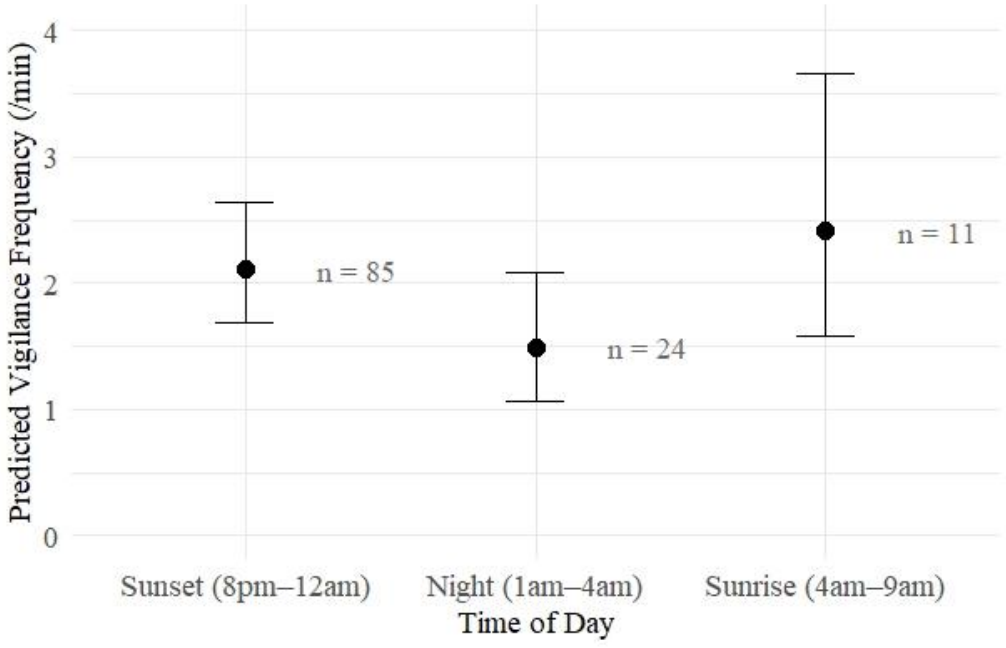

Figure 10 Predicted frequency of vigilance bouts per minute in white tailed deer on different times of day. Modelled mean estimates and 95% confidence intervals are displayed on backtransformed scale. Vigilance frequency was lowest during night and higher during twilight hours. Sample size (n) was highest on sunset observations and lowest at sunrise.

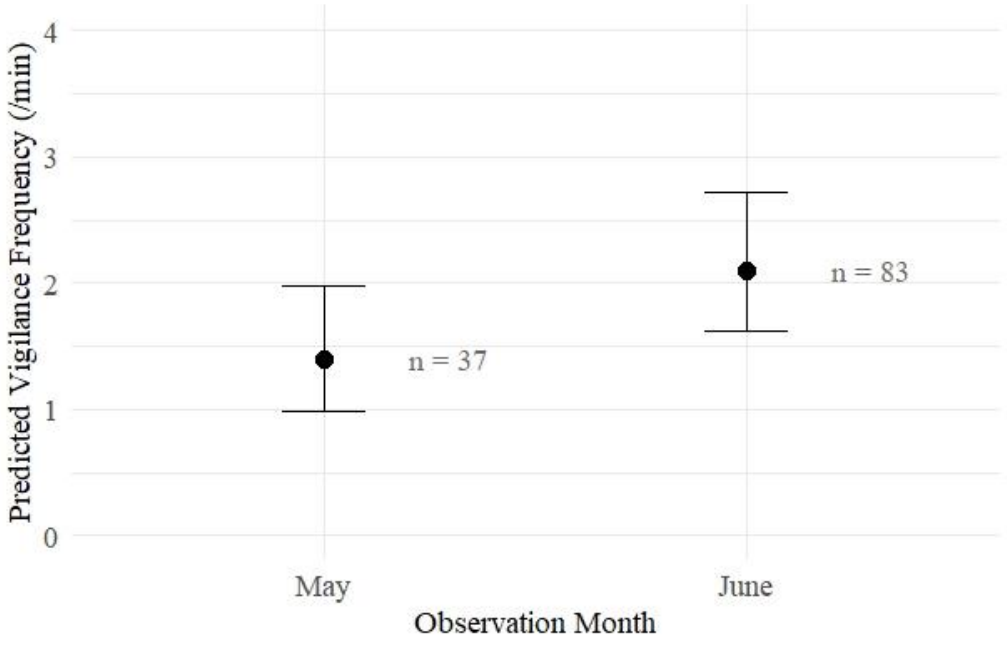

Figure 11 Predicted vigilance frequency per minute in May and June on the original count scale. Mean estimates show lower vigilance frequency in May compared to June. Means are represented with 95% confidence intervals. Sample size (n) in May was 44.5% smaller than in June.

4.1.3 Average vigilance bout duration

Average duration of vigilance bouts, modelled with a gamma distribution (log link) (Salinas Ruíz et al., 2023), was significantly influenced by time of day, while no significant effects were found in wolf presence, group size, distance from forest edge, or observation month (Table 7). Random variation was mainly explained by group identity, while spatial factors had no effects. This model was also based on the subset of 120 observations. Predicted vigilance duration was 5.6 seconds [95% CI: 3.07, 10.20] in low-risk areas and 8.0 seconds [95% CI: 5.54, 11.46] in high-risk areas.

Vigilance bouts were shortest during nighttime compared to both sunset and sunrise (Table 8 a). According to the pairwise comparisons, the difference between night and sunrise was statistically significant, showing vigilance bouts being longer during morning twilight (Table 8 b). The difference between time categories can be seen on Figure 12. The differences between sunset and other times were not significant ($p > 0.05$; Table 8 b).

Table 7 Results of gamma regression model for average vigilance bout duration. Displays fixed effects (wolf presence, group size, forest distance, time of day, month) and random effects (group ID, field study area) affecting vigilance bout duration.

Vigilance Bout Duration (s)	Wald χ^2	Df	p-value	Estimate	SE
Fixed factors					
Intercept	35.24	1	<0.001	2.18	0.37
Wolf Presence (high risk, low risk)	1.31	1	0.252	-0.35	0.30
Group Size	0.15	1	0.697	-0.33	0.08
Distance from Forest (<20 m, 20–50 m, >50 m)	0.46	2	0.794	-	-
Time of Day (sunset, night, sunrise)	7.46	2	**0.024**	-	-
Observation Month (May, June)	0.14	1	0.707	-0.10	0.26

Random effects	Variance	Std. Dev.
Study Area	0.01	0.01
Field (nested within study areas)	<0.01	<0.01
Group ID	0.28	0.53

Model fitted with gamma distribution (log link). Estimates are calculated with low risk as the reference category in the wolf presence.

Table 8 Vigilance bout duration by time of day with pairwise comparisons. (a) presents mean estimates, confidence intervals, and (b) statistical contrasts showing significantly longer bouts at sunrise compared to night.

Time of Day	Estimated model mean	SE	95% CI	
a)				
Sunset (8 p.m.–12 a.m.)	1.88	0.17	[1.55, 2.22]	
Night (1 a.m.–4 a.m.)	1.51	0.25	[1.02,2.00]	
Sunrise (4 a.m.–9 a.m.)	2.30	0.32	[1.67,2.94]	
b)				
Comparison	Estimate (log odds)	SE	z-ratio	p-value
Sunset–night	0.37	0.21	1.737	0.192
Sunset–sunrise	-0.42	0.30	-1.414	0.333
Night–sunrise	-0.79	0.30	-2.608	**0.025**

Results averaged over Wolf Presence, Distance from Forest and Observation Month. Tukey-adjusted p-values. Estimates given on the log scale.

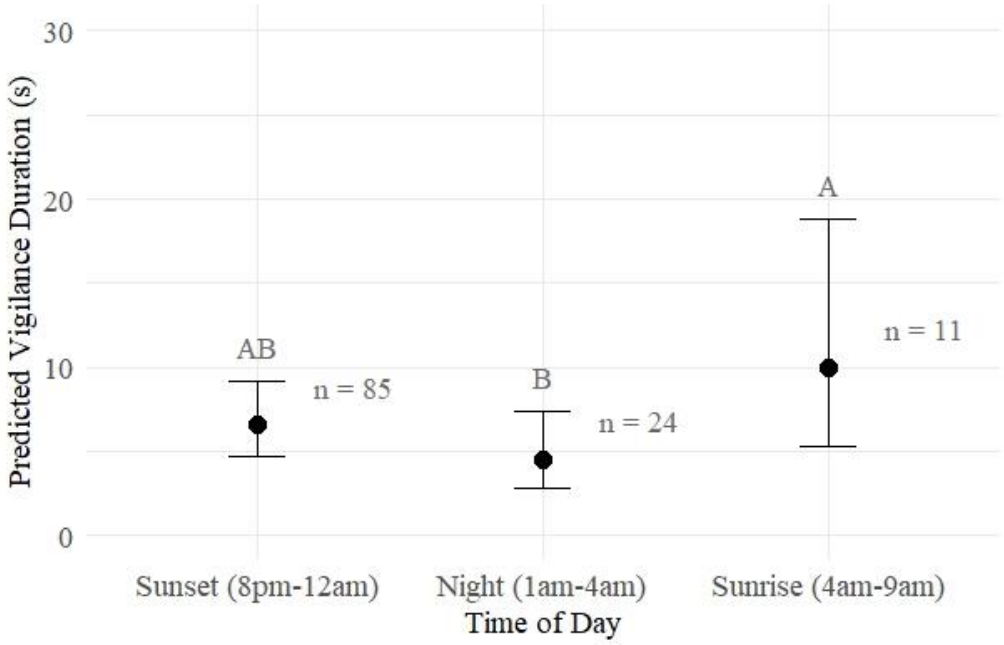

Figure 12 Average duration of vigilance bouts across times of day in white-tailed deer. Modelled values with 95% confidence intervals are shown on the original time scale (seconds). Sample size (n) varied between the time categories with fewest of observations at sunrise hours. Based on Tukey-adjusted pairwise comparisons, vigilance bout durations were significantly ($p < 0.05$) longer at sunrise (A) than night (B), while sunset (AB) did not statistically differ from either ($p > 0.05$).

4.2 Interspecific variation in vigilance behaviour under low predation risk

The descriptive statistics including both species, white-tailed deer and roe deer, showed that roe deer has lower mean at vigilance proportion and frequency. Although, the variation of these variables were higher compared to white-tailed deer (Table 9). The average vigilance bout duration was relatively similar in both species. Total sample size (N) was 83, including both species from all of the low-risk areas. However, the following models are based on sample size (n) 77 (white-tailed deer; 16, roe deer; 61), which had data on all included variables.

Table 9 Descriptive statistic of data including both study species, roe deer (*cc*) and white-tailed deer (*ov*). N = Sample size, VAR = variance, SD = standard deviation, SE = standard error.

Behaviour Variable	Species*	N	Min	Max	Mean	Var	SD	SE
Vigilance Proportion (%)								
	cc	62	0.1	53.7	19.3	179.0	13.4	1.7
	ov	21	7.8	47.9	25.7	154.0	12.4	2.7
Vigilance Frequency per minute								
	cc	62	0.4	4.6	2.0	1.0	1.0	0.1
	ov	21	1.3	5.0	2.6	0.7	0.8	0.2
Average Vigilance Bout Duration (s)								
	cc	62	2.0	17.0	6.4	11.5	3.4	0.4
	ov	21	3.0	16.0	6.8	12.1	3.5	0.8

***** *cc: Capreolus capreolus, ov: Odocoileus virginianus*

According to Wilcoxon rank-sum test, group sizes did not differ significantly (W = 503.5, p = 0.102) between white-tailed deer and roe deer in areas of low predation risk (Figure 13).

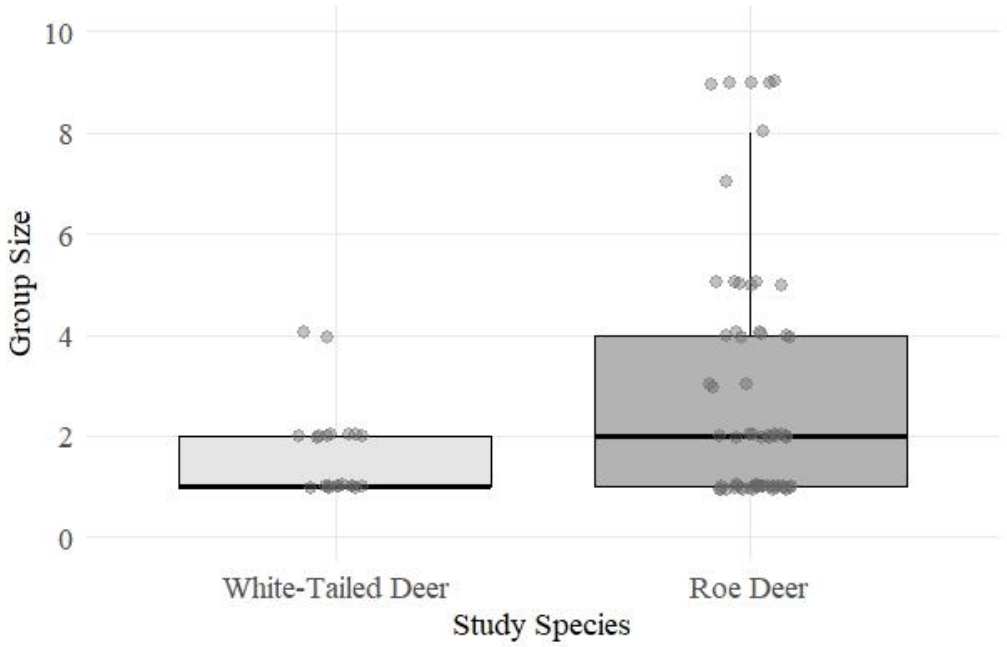

Figure 13 The group sizes of white-tailed deer (n = 21, mean ± SD = 1.67 ± 0.91) and roe deer (n = 62, mean ± SD = 2.87 ± 2.47) observed in low-risk areas. Animals observed alone were counted as a group size of one. Box-plots illustrate the spread of group sizes per species, with dots marking individual observations; the central line shows the median, boxes indicate the interquartile range, and whiskers extend to the furthest non-outlier points.

4.2.1 Vigilance proportion

Predicted vigilance proportion was 18.62% [95% CI: 8.63, 35.67] for white-tailed deer (n = 16), and 23.64% [95% CI: 14.39, 36.33] for roe deer (n = 61). Group size, distance to forest edge, or time of day showed no statistically significant main effects or species-specific interaction effects (Table 10). Therefore, results show no interspecific differences between the species. Study Field showed highest variance among the random effects, while variance in Group ID and Study Area was near zero.

Table 10 Fixed and random effects from beta regression model of vigilance proportion between roe deer and white-tailed deer in low-risk areas. Includes main and interaction terms for species, group size, forest distance, and time of day.

Vigilance Proportion	Wald χ^2	Df	p-value	Estimate	SE
Fixed factors					
Intercept	6.13	1	0.013	-1.49	0.60
Species (roe deer, white-tailed deer)	0.39	1	0.531	0.34	0.55
Group Size	0.09	1	0.764	-0.06	0.21
Distance to Forest (<20 m, 20–50 m)	2.71	1	0.100	0.61	0.34
Time of Day (sunset, night)	0.15	1	0.694	0.23	0.59
Interactions					
Group Size:Species	0.01	1	0.912	0.02	0.21
Distance to Forest:Species	1.93	1	0.164	-0.61	0.44
Time of Day:Species	0.42	1	0.518	0.41	0.63

Random effects	Variance	Std. Dev.
Study Area	<0.01	0.73
Field (nested within study areas)	0.37	0.61
Group ID	0.04	0.21

Model fitted with beta distribution (logit link). Estimates are calculated with following reference categories: Species; roe deer, Distance to Forest; 20–50 m, and Time of Day; night.

4.2.2 Vigilance frequency

A gaussian GLM model was conducted to investigate interspecific differences between white-tailed deer and roe deer. According to this model, the average vigilance frequency for white-tailed deer was 2.37 times per minute [95% CI: 1.48, 3.26; n = 16], and for roe deer 2.15 times per minute [95% CI: 1.85, 2.45; n = 61]. Model included fixed factors with species-specific interactions, and did not reveal any statistically significant predictors or differences in vigilance frequency between the species (Table 11).

Table 11 Modelled interspecific comparisons on vigilance frequency per minute between white-tailed deer and roe deer. Fixed effects include species, group size, distance to forest, and time of day, along with the interactions with the species. Random effects account for study area, nested study field, and group identity. Residuals show variation of how much of the model is not explained by fixed or random effects. No significant effects ($p < 0.05$) were found.

Vigilance Frequency (/min)	Wald χ^2	Df	p-value	Estimate	SE
Fixed factors					
Intercept	24.44	1	<0.001	2.79	0.56
Species (white-tailed deer, roe deer)	2.17	1	0.141	-0.90	0.61
Group Size	0.12	1	0.730	0.08	0.24
Distance to Forest (<20 m, 20–50 m)	0.16	1	0.693	-0.20	0.50
Time of Day (sunset, night)	0.32	1	0.573	-0.46	0.82
Observation Month (May, June)	1.11	1	0.292	-0.61	0.57
Interactions					
Group Size:Species	0.50	1	0.480	-0.17	0.24
Distance to Forest:Species	0.18	1	0.674	0.23	0.56
Time of Day:Species	1.01	1	0.314	0.88	0.87
Observation Month:Species	3.39	1	0.066	1.14	0.62

Random effects	Variance	Std. Dev.
Study Area	<0.01	<0.01
Field (nested within study areas)	<0.01	<0.01
Group ID	<0.01	<0.01
Residual (σ^2)	0.76	0.87

Model fitted with gaussian distribution (identity link). Estimates are calculated with following reference categories: Species; roe deer, Distance to Forest; 20–50 m, Time of Day; night, and Observation Month; June.

4.2.3 Average vigilance bout duration

The GLM model, fitted with gamma distribution, predicted vigilance bout duration for white-tailed deer being ~6 seconds [95% CI: 3.67, 9.77; n = 16], and ~7 seconds [95% CI: 5.64, 9.16; n = 61] for roe deer. Vigilance duration was significantly influenced by the observation month ($p < 0.05$; Table 12) across both species (n = 77). The average bout duration in low-risk areas was ~20 seconds in May (95% CI: 8.06, 50.31; n = 42), and ~11 seconds in June (95% CI: 2.99, 40.65; n = 35). Modelled interaction between species and observation month suggested some temporal variation in vigilance patterns between species, but this effect was not statistically significant ($p > 0.05$). Other predictors did not show significant differences between species or consistent effects on vigilance duration (Table 12).

Table 12 Gamma regression GLM model of average vigilance bout duration comparing roe deer and white-tailed deer. Includes main effects and species interactions with ecological variables. Sample size (n) in the model was 77.

Vigilance Bout Duration	Wald χ^2	Df	p-value	Estimate	SE
Fixed factors					
Intercept	34.56	1	<0.001	2.06	0.35
Species (white-tailed deer, roe deer)	0.08	1	0.771	-0.10	0.35
Group Size	0.98	1	0.323	-0.13	0.13
Distance to Forest (<20 m, 20–50 m)	1.62	1	0.204	0.31	0.24
Time of Day (sunset, night)	2.59	1	0.108	0.73	0.45
Observation Month (June, May)	6.03	1	**0.014**	-0.88	0.36
Interactions					
Group Size:Species	0.99	1	0.320	0.13	0.13
Distance to Forest:Species	0.36	1	0.551	-0.16	0.27
Time of Day:Species	1.98	1	0.159	-0.68	0.48
Observation Month:Species	3.66	1	0.056	0.72	0.38

Random effects	Variance	Std. Dev.
Study Area	<0.01	<0.01
Field (nested within study areas)	0.03	0.18
Group ID	0.02	0.15

Model fitted with gamma distribution (log link). Estimates are calculated with following reference categories: Species; roe deer, Distance to Forest; 20–50 m, Time of Day; night, and Observation Month; June.

5. Discussion

5.1 Overview of main findings

This study investigated the vigilance behaviour of white-tailed deer and roe deer in agricultural landscapes of South-West Finland, with a focus on the influence of wolf presence, group size, time of day, and foraging distance from the nearest forest edge. The results indicated that wolf presence marginally, but non-significantly, influenced vigilance frequency in white-tailed deer to the other direction than predicted. Wolf presence did not significantly affect any other vigilance-related variables. Similarly, distance to the nearest forest edge did not have a significant effect on vigilance. Instead, time of day emerged as consistent predictor across all vigilance metrics in white-tailed deer, with highest vigilance exhibited during twilight periods, especially at sunrise. Group size affected vigilance proportion and frequency, so that lower vigilance levels were exhibited in larger groups. Additionally, vigilance frequency in white-tailed deer was lower in May compared to June. The interspecific comparisons revealed no significant differences in vigilance behaviour between the species, although roe deer tended to show slightly higher mean vigilance levels across variables. Within both species in low-risk areas the average vigilance bout duration was significantly affected by observation month, but it did not highlight any interspecific differences.

5.2 Vigilance responses to predation risk and group-level effects in white-tailed deer

Contrary to the primary hypothesis of deer increasing their vigilance in the presence of predator (Lima & Bednekoff, 1999b), white-tailed deer did not exhibit significantly higher vigilance levels in areas with wolf presence (high-risk areas). Although predator presence marginally affected vigilance frequency, the effect was in the opposite direction than expected: vigilance appeared being lower in high-risk areas. Overall, the lack of a significant difference in vigilance levels may reflect a reliance on habitat-based risk management or an insufficient stimulus to trigger a measurable behavioural response (Beauchamp, 2015). It should be noted that the sample sizes were unequal between the risk areas and particularly low in low-risk areas, which reduced statistical power. Nevertheless, the available data did not suggest the existence of differences. However, as previously mentioned, wolves have only recently recolonised the study region and might not yet impose strong enough selection pressure to generate a Landscape of Fear that could be detected through altered vigilance levels (Zanette & Clinchy, 2025). Furthermore, the study areas were chosen based on mapped illustrations of wolf territories during the

preceding winter (Valtonen et al., 2024) rather than confirmed wolf presence or activity during the study period, meaning that some observed individuals, particularly in high-risk areas, may not have encountered wolves or signs of their presence. This result may also reflect similar patterns with the central hypothesis of Dellinger et al. (2019), suggesting that white-tailed deer primarily manage predation risk through "fine-scale shifts" in habitat use, rather than broad-scale avoidance or a generalized increase in vigilance. Given their flight strategy based on early detection and sprinting, white-tailed deer may select microhabitats that optimise their escape potential rather than investing energy in vigilance. The decision to conduct this study on open agricultural fields, which provide flat terrain and usually high visibility, supports this interpretation.

Group size on the other hand was a significant predictor of both vigilance proportion and frequency in white-tailed deer, supporting the Many Eyes Hypothesis (Pulliam, 1973). Individuals in larger groups showed lower vigilance, which indicates of a shared detection benefit. This pattern aligns with prior findings across diverse ungulate groups (Fitzgibbon, 1990b; Lashley et al., 2014; Fattorini & Ferretti, 2019). It should be noted, that the average group size was slightly larger in high-risk areas, which could affect the detected marginal effect of vigilance frequency being lower on high-risk areas compared to low-risk areas. Also, results were not consistent with the hypothesis that vigilance would decrease in more open areas further from cover (Elgar, 1989), as none of the vigilance variables were influenced by foraging distance from the forest. Here, the interaction between group size and the predator presence, as well as foraging distance from forest and study area would have been interesting to investigate, but my data did not allow these additions in the model.

5.3 Temporal variation in vigilance

Time of day also significantly influenced vigilance behaviour in white-tailed deer. Vigilance was lowest during night compared to twilight periods, in all vigilance-related variables. Increased vigilance during sunset and sunrise may reflect risk-sensitive foraging strategies adapted to increased predator or human activity. Notably, vigilance bouts were also significantly longer at sunrise than at night, suggesting a behavioural mechanism for enhanced risk assessment in the shift to a higher risk timeframe. Previous research has shown that wolves are most active at dawn and dusk, with increased movement and predation rates during these times (Theuerkauf et al., 2003; Theuerkauf, 2009; Ferreiro-Arias et al., 2024). Wolves may also shift their behaviour to increased nocturnal activity in response to human presence (Theuerkauf,

2009; Ferreiro-Arias et al., 2024; Sunde et al., 2024). Similarly, cervids have been observed to modify their behaviour and diel patterns in response to the perceived risk posed by humans (Sönnichsen et al., 2013; Bonnot et al., 2020; Proudman et al., 2020). Interestingly, Theuerkauf et al. (2003) suggest that human influence on wolf activity may be indirect, driven by changes in prey behaviour, which in turn could affect wolf movement and hunting strategies.

Observation month significantly affected vigilance frequency, but not vigilance bout duration in white-tailed deer. White-tailed deer tended to have more vigilance bouts in June compared to May. This could indicate the need to scan surroundings more often when the vegetation is taller and denser, both in the open field and forest edge. Another possible explanation regarding higher vigilance frequency in June could be the fawning season (Lashley et al., 2014; Costelloe & Rubenstein, 2018; Poutanen et al., 2022). Fawns at this time of year are small, and especially white-tailed deer hide their fawns well in the cover of tall vegetation. However, the presence of fawns could not be confirmed in this study. One addition could have been to repeat this study in autumn when fawns are a bit more independent, which may also affect vigilance dynamics within a group (Higdon et al., 2019).

An important consideration not captured in this study is the potential seasonal variation in both predator activity and human disturbance. For instance, wolves are likely to exhibit seasonal variation in activity and territory use, which may influence the degree of predation risk perceived by prey species (Lodberg-Holm et al., 2021). Similarly, human hunting pressure during the autumn may alter deer vigilance patterns, either by increasing overall alertness or shifts in habitat use across the landscape (Benhaiem et al., 2008; Proudman et al., 2020). Conducting this study during the hunting season would help reveal how temporal fluctuations in predator presence and human disturbance shape vigilance behaviour, and whether deer alter their strategies of risk assessment in response.

5.4 Interspecific comparison

In low-risk areas, interspecific comparisons revealed no significant differences between roe deer and white-tailed deer across any vigilance-related variables. While roe deer appeared to show slightly higher mean vigilance proportion and longer vigilance bouts, these differences were not statistically significant. These findings suggest that both species may exhibit similar vigilance strategies in areas with lower wolf abundance and under similar ecological conditions (Bartos et al., 2002)

Despite these observed similarities, species-specific differences in habitat preference and anti-predator strategies could still influence behavioural responses. White-tailed deer have been shown to use open fields, where it can rely on early detection and rapid escape (LaGory, 1987; Dellinger et al., 2019), while roe deer is considered a woodland species, which can adapt to fragmented and human dominated landscapes by utilizing hedgerows if forest habitats are scarce (Morellet et al., 2011). Moreover, roe deer may show shorter risk assessment intervals and earlier flight responses in open habitats (Bonnot et al., 2017). These differences may partially explain the slightly higher vigilance observed in roe deer. However, it remains to be studied to what degree these two ungulate species compete for habitats and resources. Previous research on roe deer and white-tailed deer living in same areas found very few aggressive encounters, suggesting minimal direct competition between these species, and instead, a tendency toward coexistence or even cooperative use of shared habitats (Bartos et al., 2002).

Interestingly, the group size effects observed in the white-tailed deer-specific models were not apparent in the interspecific comparisons. This may reflect variation in group structure between the species or risk areas, or lack of statistical power due to smaller sample sizes in interspecific models. Similarly, while time of day was a significant predictor in white-tailed deer specific models, no such effects were detected when comparing the two species, likely due to merged time categories (e.g. sunrise pooled with night) and limited sample sizes. This result could also indicate that prey has no reason to adapt vigilance levels according to the time of day in areas where wolf is nearly absent (Theuerkauf, 2009; Ferreiro-Arias et al., 2024), although lynx might still be present.

Finally, the relatively high amount of variance explained by group identity in interspecific model suggests that within-group dynamics may have a stronger influence on vigilance bout duration than species identity alone under low-risk conditions. This could indicate of contagious vigilance between group members (McDougall & Ruckstuhl, 2018) or other social hierarchies within groups, such as presence of males in female dominated group (Fitzgibbon, 1990b; Lashley et al., 2014; Cherry et al., 2015).

5.5 Data limitations and methodological considerations

All findings presented in this thesis must be interpreted with caution, especially due to the asymmetric data distribution between species across predation risk context. Only 13.3% of all observed white-tailed deer individuals were observed in low-risk areas. In low-risk areas 20.8%

of observations consisted of white-tailed deer while the rest of the observations were of roe deer. The relatively small sample size of white-tailed deer in low-risk areas may have limited the statistical power of the models.

As roe deer were nearly absent from high-risk areas within wolf territories, full interspecific comparisons on the effects of wolf presence on vigilance behaviour could not be conducted. The reason for such a low number of observed roe deer can only be speculated. One possibility is that roe deer actively avoid open habitats within wolf territories, and the study's restricted focus on agricultural fields may have limited the possibility to detect them (Morellet et al., 2011; Bonnot et al., 2017). Alternatively, roe deer may effectively avoid inhabiting areas where wolf territories have recently established. It is also possible that lynx, a key predator of roe deer, avoids these areas too. This would concentrate lynx presence in low wolf-risk areas, where it would make forest cover riskier for roe deer. If this were the case, it would explain why roe deer were observed more frequently in open fields in low-risk areas. However, there is no recent evidence to support such avoidance behaviour between these two predators (Schmidt et al., 2008). Another explanation would be that wolves have preferentially established in areas with higher densities of white-tailed deer, which can serve as more profitable prey, similarly to the pattern observed with red deer in Germany (Roder et al., 2020).

Furthermore, there are several methodological improvements that could have elevated the scientific level of this thesis. Firstly, this study did not include direct measures of individual deer characteristics such as age, sex, or reproductive status, each of which could influence vigilance behaviour (Elgar, 1989; Lashley et al., 2014). All observed animals were adults, but it could not be specified whether they were young or old. Sex was recorded in field, but the problem in detecting antlers from video material left the data very imbalanced. Eventually, the variable contained many missing values, which was the reason it was not used in the analyses. Also, it could not be verified whether individuals had been observed earlier, which could create pseudoreplication by unintentional repeated measures of vigilance behaviour of the same individuals on different days or within different groups on same study fields. In addition, social variables beyond group size, such as the presence of fawns, alarm signals or mixed-species groups, were not recorded, but may have influenced the within-group variation of vigilance behaviour (LaGory, 1987; Reby et al., 1999; Bartos et al., 2002; Costelloe & Rubenstein, 2018;). Moreover, predator presence data lacked precision. Wolf presence was based on broad territory maps (Valtonen et al., 2024) rather than confirmed activity during the study period. Lynx presence

was assumed constant due to the absence of spatial data, even though national assessments provide visual estimates of the distribution of female lynx home ranges derived from cub observations (Herrero et al., 2024).

With respect to video monitoring, Reolink cameras did not serve the study purposes as well as the other surveillance cameras. It would thus be recommendable to employ only the larger camera setup in future. The telescope with a phone adapter worked very well, as the observer could make audio notes (with a lowered voice) on the videos of factors happening outside of the camera frame, such as people walking by, or how many individuals were on the field at the time of observation bout. However, working with the telescope takes time and effort, and requires a careful approach, so that animals would not detect the observer.

Future studies should incorporate more fine-scale metrics of habitat characteristics and both predator and human disturbance, by potentially including distance to the nearest roads and buildings, or even use GPS tracking to collect more information of the movement patterns and habitat use of both predator and prey (Vander Vennen et al., 2016; Kröschel et al., 2017; Sunde et al., 2024). Also, social composition and hierarchy within animal groups should be considered as an explanatory variable in studying vigilance patterns (Elgar, 1989). A knowledge gap about the distribution and habitat choices of roe deer in Finland should be studied, as well as, the aspects of competition between roe deer and white-tailed deer. Also, the percentage of these two cervid species should be investigated in wolf diet, especially in this part of Finland.

6. Conclusions

This thesis demonstrates that in agricultural and human-dominated landscapes, vigilance in small cervids is shaped more strongly by social and temporal factors than by predator presence. Group size, time of day, and observation month influences vigilance in white-tailed deer, whereas wolf presence had no significant effect. In areas of low wolf density, vigilance patterns were similar for both roe deer and white-tailed deer, suggesting that under similar ecological conditions, the two species display broadly similar vigilance strategies. These findings highlight the importance of ecological and anthropogenic factors in shaping anti-predator behaviour. Future research should focus on the role of human disturbance, predator-prey dynamics, and interspecific competition, to improve understanding of behavioural adaptations in landscapes with recolonising predators.

Acknowledgments

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OpenAI's ChatGPT model (GPT-4, 2025) was utilised in language management, R-code optimisation in statistical analysis and in visualising the results.

Appendices

Appendix 1: Study fields in high-risk areas

Study fields in high-risk areas marked with orange polygons. The polygon outlines represent the approximate area from which observations were collected using the camera system, and therefore do not always cover the full field area. Dot marks the placement of the camera, which could be remotely rotated 355–360°.

Appendix 2: Study fields in low-risk areas

Study fields in low-risk areas marked with orange polygons. The polygon outlines represent the approximate area from which observations were collected, and therefore do not always cover the full field area. In Ruissalo (L1), the observations were conducted with telescope or binoculars from covered place under the current wind direction. In study areas L2–L5, dot marks the placement of the surveillance cameras which could be remotely rotated 360°.