

Temporal interactions of Finnish mesopredators based on camera trap data

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The introduction of a new species outside their natural range can cause significant changes to an ecosystem. Especially invasive predators have been found to be harmful. The raccoon dog (*Nyctereutes procyonoides*), introduced to regions near Finland, spread to the country in the 1950s. It is now spread across most of the country and is the most common mesopredator in southern Finland. Many negative impacts have been associated with the spread of this species. One of the presented impacts caused by the raccoon dog is competition with local mesopredators. In this thesis I aim to investigate the interactions between the raccoon dog, the red fox (*Vulpes vulpes*) and the Eurasian badger (*Meles meles*).

Using camera trap data collected in Finland in February and March of 2024, I studied the diel activity patterns of the focal species, the time each species spent in front of the camera traps, as well as how the presence of the red fox and the Eurasian badger might affect the behaviour of the raccoon dog. The camera traps were located in areas surrounding wetlands and each separate site had from one up to 19 cameras. In total there were 74 locations around Finland with 352 camera traps, some of which contained an attractant – a carcass, a feeder or a trap – to lure animals to the site. Diel activity of the species was inspected using diel activity plots and the time species spent in front of cameras was analysed using a generalised linear mixed model. For the effects that the red fox and the Eurasian badger might have on the raccoon dogs' presence a linear mixed model was used to see whether the presence of other species altered the time it took raccoon dogs to arrive at the camera trap site.

I found that all three focal species showed predominantly nocturnal activity. While raccoon dogs and Eurasian badgers were quite strictly nocturnal, the red fox was more flexible and used also daylight hours, although preferring nighttime. Attractants were not found to affect the diel activities of the focal species. In sites where all species occurred, Eurasian badgers spent the longest time in front of the cameras indicating dominance over the two smaller species. Lastly, when a site had an attractant and other focal species were present, the raccoon dog was found to change its behaviour to arrive earlier to the site. This was statistically significant when the red fox was present, showing that the raccoon dog might not avoid the red fox but becomes more active when foxes were present.

Given the increasing raccoon dog population and declining red fox numbers in Finland, these results suggest that raccoon dogs may gain competitive advantage through behavioural flexibility. The final result of this thesis shows, that raccoon dogs are able to change their behaviour depending on the presence of other species. In addition, all three focal species were predominantly nocturnal, with Eurasian badgers spending the longest time at camera sites — likely indicating a hierarchical relationship shaping the mesopredator community. As the warming climate is likely to facilitate the expansion of raccoon dogs into more northern regions of Finland, understanding the interactions of raccoon dogs with native species remains essential for conservation of the native species and management of this invasive species.

Keywords: interspecies interactions, mesopredators, behavioural flexibility, raccoon dog, invasive species

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Lajien levittäytyminen niiden alkuperäisen levinnäisyysalueen ulkopuolelle voi aiheuttaa useita muutoksia ekosysteemeissä. Varsinkin vierasperäisten petoeläinten on havaittu usein aiheuttavan ongelmia paikallisille ekosysteemeille. Supikoira (*Nyctereutes procyonoides*) levisi Suomeen 1950-luvulla ja on nyt yleisin keskikokoinen peto suuressa osassa maata. Lajin leviämiseen on liitetty useita haitallisia vaikutuksia, kuten kilpailu paikallisten petoeläinten kanssa. Tässä tutkielmassa tarkastelen supikoiran, ketun (*Vulpes vulpes*) ja mäyrän (*Meles meles*) välisiä vuorovaikutuksia.

Aineistona käytin Suomessa helmi- ja maaliskuussa 2024 kerättyä riistakamera-aineistoa tutkiakseni tutkimuslajien vuorokausiaktiivisuutta, lajien kameran edessä viettämää aikaa sekä sitä, miten ketun ja mäyrän esiintyminen saattaa vaikuttaa supikoiran käyttäytymiseen. Kameran oli sijoitettu kosteikkojen läheisyyteen siten, että yhden kosteikon ympärillä oli yhdestä 19 kameraa. Tutkimusalueita oli yhteensä 94 ympäri Suomea ja kameroita 352, joista suurimman osan edessä oli raato, ruokintalaite tai loukku, eläinten paikalle houkuttelemiseksi. Tarkastelin tutkimuslajien vuorokausiaktiivisuutta kuvaajien avulla ja lajien kameran edessä viettämää aikaa analysoin yleistetyllä lineaarisella sekamallilla. Lisäksi ketun ja mäyrän mahdollista vaikutusta supikoiran läsnäoloon selvitin lineaarisella sekamallilla käyttäen. Tarkoitukseni oli tutkia vaikuttiko muiden lajien läsnäolo supikoirien saapumisaikaan riistakameroiden luokse.

Tulokseni osoittavat, että kaikki kolme tutkimuslajia olivat pääosin yöaktiivisiä. Siinä missä supikoirat ja mäyrät olivat lähes pelkästään yöaktiivisiä, kettu oli kuitenkin joustavampi vuorokausiaktiivisuudessaan ja liikkui myös päiväsaikaan, vaikka suosikin yöaikaa. Houkuttimilla en havainnut olevan vaikutusta kohdelajien vuorokausiaktiivisuuteen. Alueilla, joissa havaitsin kaikki kolme kohdelajia, olivat mäyrät pisimpään kameroiden edessä. Tämä viittaa mäyrän mahdolliseen dominoivaan asemaan kahta pienempää petoa kohtaan. Lisäksi kohteilla, joissa oli sekä houkutin että muita havaittuja tutkimuslajeja, havaitsin supikoiran muuttavan käyttäytymistään siten, että se saapui paikalle aikaisemmin, kun toisen lajin yksilö oli alueella. Tulos oli merkitsevä, kun toinen eläin alueella oli kettu, mikä saattaa viitata siihen, ettei supikoira välttä kettua, vaan voi muuttua aktiivisemmaksi sen läsnäollessa.

Supikoirat voivat saada kilpailuedun siitä, että ne kykenevät mukauttamaan käyttäytymistään eri olosuhteissa. Tämä on mahdollisesti edesauttanut Suomen supikoirakannan kasvua siinä missä kettukannan taas on havaittu pienenevän. Kaikki kolme lajia olivat pääosin yöaktiivisiä ja se, että mäyrät viettivät pisimmän ajan kameroiden edessä saattaa indikoida lajien välistä hierarkiaa, joka vaikuttaa lajien yhteisesiintyvyyteen. Ilmaston lämpenemisen seurauksena supikoiran odotetaan levittäytyvän yhä pohjoisemmaksi, jolloin lajien välisten vuorovaikutusten ymmärtäminen on keskeistä alkuperäislajiston suojelun sekä vieraslajin hallinnan kannalta.

Avainsanat: lajien väliset vuorovaikutukset, keskikokoiset pedot, joustava käyttäytyminen, supikoira, haitallinen vieraslaji

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1 Introduction

1.1 Interspecies interactions and ecological niches

In the wild, animals face competition for different resources such as food, habitats and nesting sites, both within the same species, as well as between different species (Amarasekare, 2003). Competition is often strongest among animals with similar characteristics and life histories, as they tend to use the same resources and habitats (Amarasekare, 2003). To coexist in the same environment, interspecific (between species) competition must be weaker than intraspecific (within species) competition (Amarasekare, 2003). This can be achieved through niche differentiation, meaning that species reduce competition by using resources in different ways. This differentiation can be separated into three main strategies in competition avoidance: spatial niche partitioning, temporal niche partitioning and resource partitioning (Amarasekare, 2003; Monterroso et al., 2014).

For example, a study conducted by Wereszczuk and Zalewski (2015) found that very similar species, stone marten (*Martes foina* Erxleben, 1777) and pine marten (*Martens martens* Linnaeus, 1758), show a possibility of a strong ecological niche segregation by the species using nearly completely different habitats. The niche segregation allowed the species to cohabit the same area without exclusion of the other species. This can be interpreted as spatial niche segregation as the similar species cohabit the same area but use different habitats. While the study (Wereszczuk & Zalewski, 2015) found only weak results about temporal segregation between the stone and pine marten, other predators have been found to also separate their resource use around the diel – 24 hour – cycle to minimise competition and to foster coexistence (e.g. Di Bitetti et al., 2009; Monterroso et al., 2014). For instance, mesopredator coexistence has been found to be facilitated by temporal niche partitioning, especially in more complex communities (Monterroso et al., 2014). While the species have their preferred periods for activity, they can also show temporal flexibility to minimise competition as well as to maximise their access to needed resources (Monterroso et al., 2014).

In addition to spatial and temporal niche partitioning, other traits – such as species-specific resource use and physical traits, like body size, also affect interspecies interactions and competition. For instance, larger predators can prevent smaller predators from accessing shared food resources, such as carcasses (Donadio & Buskirk, 2006). Body size and dietary overlap are closely linked to competitive interactions among carnivores (Lovari et al., 2013). When

species differ in body size, competition is reduced because they typically target different prey, lowering the likelihood of resource overlap (Donadio & Buskirk, 2006; Lovari et al., 2013). However, when predators of similar size use the same resources, the frequency of food-related interactions tends to remain constant or increase as these predators also share habitats and encounter one another more frequently, which leads to more opportunities of confrontation and competition (Donadio & Buskirk, 2006).

Understanding niche partitioning is vital for interpreting how species interact as it can show how species share and reduce competition for limited resources (Amarasekare, 2003). These interactions between two or more species can play a key role in the successful conservation of both species and their habitats as they can influence ecosystem stability and trophic dynamics. Recognising how species interact is particularly important when new species are introduced outside of their natural range, as this can trigger a variety of responses among native species and disrupt ecosystem functioning (Pyšek et al., 2020).

1.2 Invasive alien species

Ecosystems have been significantly disrupted by human actions, particularly through habitat fragmentation and the spread of invasive alien species, which are two major drivers of global biodiversity loss (Dirzo & Raven, 2003; Doherty et al., 2016; Pyšek et al., 2020). Invasive species, often introduced accidentally through global trade and travel, are becoming increasingly common and pose serious threats to ecosystems as well as to individual species (Paulomäki et al., 2023; Pyšek et al., 2020). For example, invasive terrestrial animal species in Europe, such as the American mink (*Neogale vison* Schreber, 1777), the Norway rat (*Rattus norvegicus* Berkenhout, 1769) and the Canada goose (*Branta canadensis* Linnaeus, 1758), prey on native species, spread diseases and may hybridise with native species (Keller et al., 2011; Scalera et al., 2012). Overall, due to human impact, alien species have spread around the globe and have been found to be a growing threat to nature, as well as to the ecosystem services provided by nature (Paulomäki et al., 2023). Climate change can also facilitate the invasions and increase the number of high-risk invasive alien species (Solarz et al., 2023).

Native species have an evolutionary history in a particular region and are considered natural in the local ecosystem. Alien species, on the other hand, are introduced either on purpose or by accident by humans (Vieraslajit.Fi, 2021). When an alien species becomes established and is considered to cause significant harm to biodiversity, ecosystem services or human health, it is classified as invasive (European Commission, 2014; Roy et al., 2023). For example, the

European Union (EU) has adopted a regulation on invasive alien species (European Commission, 2014) and lists species that are considered invasive. While not all alien species become invasive, the probability of that happening is linked to different characteristics such as high fecundity, mobility and ecological plasticity (David et al., 2017). However, when species arrive to a site on their own accord they are considered as immigrant species and not as alien species, thus the status of these species is different (Vieraslajit.Fi, 2021).

Predator species can be especially harmful when introduced outside of their natural range (Doherty et al., 2016; Salo et al., 2007). Invasive predators have been found to suppress native prey species more than native predators do, leading to more vulnerable prey populations (Salo et al., 2007). Thirty invasive mammalian predator species are discovered to be responsible for extinction or endangerment of 738 species globally (Doherty et al., 2016). These impacts highlight the threats that invasive predators pose to biodiversity and ecosystems, showing the importance of monitoring and managing their spread.

1.2.1. Raccoon dog as an invasive mesopredator in Finland

The common raccoon dog (hereafter referred to as raccoon dog, *Nyctereutes procyonoides* Gray, 1834) and the American mink are the two invasive mammalian predators that have become established in Finland (Holmala, 2016; Holmala & Kauhala, 2019). Both have negative impacts to the native species in Finland such as predation especially in islands and spreading of diseases (Holmala, 2016; Holmala & Kauhala, 2019) and, therefore, have been classified as harmful. Raccoon dogs have been listed as harmful alien species by the European Union in 2017 (European Commission, 2017) due to the threat caused by predation on waterfowl and amphibian species, as well as the spreading of diseases. The American mink is also spreading in Europe (Vada et al., 2023) and it was classified as a harmful alien species by the European Union in 2025 (European Commission, 2025).

The raccoon dog was brought from East Asia to western Russia in the early 20th century in hopes for a new fur animal (Kauhala & Kowalczyk, 2011). The animals were released into the wild in several places in western Russia as well as elsewhere in Europe such as Estonia and Karelia Isthmus (Kauhala & Kowalczyk, 2011). In Finland, the colonisation started slowly in the 1950s, but by the mid-1970s most of southern and middle of Finland was habited and now the raccoon dog is the most common mesopredator in the country (Kauhala, 2007; Kauhala & Kowalczyk, 2011). Raccoon dog populations have been increasing ever since their first introduction to Europe and there has been multiple presented effects to local fauna (Kauhala &

Kowalczyk, 2011). The rapid rise in raccoon dog numbers can be explained by their attributes which are common in invasive species: high fecundity (on average of 8-10 pups), mobility (juveniles often disperse away from their parents' home range and can travel long distances) and opportunistic diet (scavenging omnivory) (Kauhala & Kowalczyk, 2011; Scalera et al., 2012). In colder climates raccoon dogs hibernate, which allows them to avoid colder months while still enabling them to inhabit northern parts of Europe (Kauhala & Kowalczyk, 2011). Beside their diet, the opportunistic characteristics of raccoon dogs can be seen in hibernation, since they are known to use badger setts for wintering and as breeding dens (Kauhala & Kowalczyk, 2011; Kowalczyk et al., 2008).

It has been presented that raccoon dogs can harm native species (Scalera et al., 2012). Potential negative impacts are, for example, increased competition between mesopredators, predation on amphibians and on the eggs of ground nesting waterfowl (Holopainen et al., 2021; Kauhala & Kowalczyk, 2011; Scalera et al., 2012). The results have not been fully conclusive. For example, the assertion that raccoon dogs specialise in predation on waterfowl eggs was not supported in a study that found a low occurrence of waterfowl DNA in the raccoon dog diet during the breeding season of waterfowl (Tuomikoski et al., 2024). However, in an experiment where raccoon dogs and American minks were removed from nesting islands of eiders in the Finnish archipelago, the results found that the nesting success increased when the invasive predators were removed (Jaatinen et al., 2022).

While the diet of raccoon dogs has been extensively studied, the effects that native mesopredators have on the raccoon dog behaviour are less known. A study conducted in northeast Germany by Drygala and Zoller (2011) showed that raccoon dogs and red foxes (*Vulpes vulpes* Linnaeus, 1758, hereafter referred to as fox) can coexist in the same area with home ranges that overlapped on average by more than 25%. However, it remained unclear whether this overlap influenced interactions between the two species, but such overlap suggests that these species can tolerate each other spatially and cohabit the same areas (Drygala & Zoller, 2013; Schwemmer et al., 2020). Moreover, their coexistence does not necessarily prevent competition. In Finland a study about predator removal on waterfowl breeding success found that when the number of raccoon dogs decreased due to hunting the number of foxes increased in the same area (Kauhala, 2004). This indicates that there is possible competition between raccoon dogs and foxes, as a reduction in one species appears to benefit the other. The competition is quite possible as they have similar diets and both can use burrows dug by the Eurasian badgers (*Meles meles* Linnaeus, 1758, hereafter referred to as badger) (Kowalczyk et

al., 2008; Mori et al., 2015; Nowakowski et al., 2020). In addition, the spread of diseases from raccoon dogs to foxes can also be a possible reason for the rise of foxes in the absence of raccoon dogs.

Direct competition between badgers and raccoon dogs has perhaps not been studied as much as possible competition between the fox and the raccoon dog. Nevertheless, interspecies interactions have been recorded, especially in the context of badger setts. Badgers have been recorded to kill raccoon dog cubs and possibly adults that are using badger setts (Kowalczyk et al., 2008). On the other hand, killing of badger cubs by raccoon dogs and foxes have also been recorded (Rotenko & Sidorovich, 2017). In Belarus, the decline of the badger population has been presented to be partly due to the presence of raccoon dogs and the competition between the two species (Rotenko & Sidorovich, 2017). For example, in the late winter and early spring, raccoon dogs and badgers have been found to compete for carcasses that are an important food source for both of the species at that time of the year (Rotenko & Sidorovich, 2017).

As the raccoon dog, the fox and the badger share common traits and use similar resources, interspecies interactions are unavoidable and the presence of one species affects the behaviour of the other two species (Barrull et al., 2014; Elmeros et al., 2018; Macdonald et al., 2004; Oerlemans & Koene, 2008). Fox populations have been found to decrease, with the most noticeable declines in the southern Finland, whereas the population densities of raccoon dogs have increased, especially in the northern limit of distribution (Selonen, et al., 2024b). While it is unclear whether the growing populations of raccoon dogs have affected the decline of foxes and what other impacts they might have, it is important to study the interaction between these species.

1.3. Aims of the study

In this master's thesis, I study the interactions between the badger, the fox and the raccoon dog using camera trap data collected in Finland. The study focuses on three main aims:

1. To analyse the diel activity patterns of the focal species. I expect to find the badger, the fox and the raccoon dog to mostly express nocturnal activity. This hypothesis is supported by previous studies that researched the activity times of these species (e.g., Kowalczyk et al., 2003; Monterroso et al., 2014; Schwemmer et al., 2021; Zoller & Drygala, 2013). I also test if food availability, in the form of bait in front of the camera

traps affect the temporal activity of the study species. The possible differences in diel activity can indicate how species partition time to reduce interspecific competition.

2. To assess how long each species spends in front of camera traps. I expect the larger species, the badger, to spend more time at the sites due to their dominant behaviour and competitive advantage, while raccoon dogs and foxes may spend less time, potentially avoiding direct encounters.
3. To inspect how the presence of native species, the badger and the fox, affects the arrival times of the invasive raccoon dog. I anticipate raccoon dogs to delay their arrival when badgers or foxes are present to avoid and minimise conflict and competition. Examining this relationship between the species could disclose whether the invasive raccoon dog adjusts its behaviour in response to the native species.

2 Material and methods

2.1 Target species

Mesopredators are most often medium-sized predators that in trophic levels are placed in the middle as they prey on smaller animals and can be prey to bigger apex predators (Prugh et al., 2009). The status of a mesopredator can differ depending on the environment. In the absence of true apex predators – such as grey wolves (*Canis lupus* Linnaeus, 1758) – the prevailing mesopredators can claim the spot as an apex predator (Prugh et al., 2009). Mesopredators can be, for example, coyotes or medium-sized birds of prey, such as the Eurasian sparrowhawk (*Accipiter nisus* Linnaeus, 1758). In Finland, the most common mesopredators are the raccoon dog, the badger, the fox and the European pine marten. Land mammals that are considered to be apex predators in Finland are the grey wolf, the brown bear (*Ursus arctos* Linnaeus, 1758), the Eurasian lynx (*Lynx lynx* Linnaeus, 1758) and the wolverine (*Gulo gulo* Linnaeus, 1758). The white-tailed eagle (*Haliaeetus albicilla* Linnaeus, 1758) and the golden eagle (*Aquila chrysaetos* Linnaeus, 1758) can also be classified as apex predators in Finland.

The focal species of this study are the badger, the fox and the raccoon dog (Figure 1). These three species are relatively alike in their weight (on average 5-10 kilograms, with the fox being the lightest and the badger the heaviest) and in their habitat use, as well as in their diet. These animals share similar niches which makes competition possible and the spreading of the raccoon dog might have consequences to the native mesopredators as well as to other species. The outcomes for the local mesopredators can be varied, such as less den sites and feeding opportunities (Kauhala & Kowalczyk, 2011). However, as the interaction is not only one-sided, the native mesopredators can also influence raccoon dog presence, for example by cub killings (Kowalczyk et al., 2008).



Figure 1. a) The Eurasian badger (*Meles meles*), b) the red fox (*Vulpes vulpes*) and c) the raccoon dog (*Nyctereutes procyonoides*) as seen in camera trap pictures. Traits that can help in recognition are for example colouring, body and tail shape and size.

In Finland, foxes, badgers and raccoon dogs can be mostly found in southern and central Finland with some irregular sightings of raccoon dogs and a sparse population of foxes within Lapland. While all three animals inhabit the same areas, they prefer different habitat types and this preference can change according to the seasons. Generally, raccoon dogs favour habitats with abundant undergrowth such as woodlands, for example mature spruce forests and young pine forests, as well as meadows and gardens (Holmala & Kauhala, 2009; Kauhala & Auttila, 2010). In contrast, badgers prefer various kinds of forests that have thick canopy but less vegetation on ground level (Kauhala & Auttila, 2010). Foxes, on the other hand, do not seem to avoid or prefer any specific habitat type over another, but their most common habitats have been found to be young pine forests, mature pine and spruce forests and fields (Holmala & Kauhala, 2009). Home-range sizes range roughly from 1.5 square kilometres up to 10 square kilometres, with badgers having the biggest home ranges and raccoon dogs the smallest (Holmala & Kauhala, 2009). Between the three species the winter activity varies as foxes are active through whole winter, badgers usually awake in March after winter dormancy and raccoon dogs can be asleep for short periods when the weather drops below -10°C (Kauhala et al., 2007; Selonon, et al., 2024c).

Raccoon dogs have been found to use the same major dietary components as foxes and badgers while still being more opportunistic and owning a wider dietary niche (Elmeros et al., 2018). With badgers' diet the raccoon dog shares invertebrates and cereals and with foxes' diet birds and fruits (Elmeros et al., 2018). Foxes, while also being opportunistic omnivores, tend to be more predatory than raccoon dogs as they feed frequently on birds and small mammals like voles and hares (Dell'Arte et al., 2007). All three use small mammals and carrion as important sources of food (Elmeros et al., 2018; Gomes et al., 2020; Tuomikoski et al., 2024).

2.2 Camera trap data

Data used in this study was obtained from camera trap photos that were taken in Finland in February and March of 2024. The data was collected in collaboration with Metsähallitus and the Finnish Wildlife Agency as a part of the Helmi habitats protection program. One of the aims of the project was to improve the conservation of endangered waterfowl near important bird breeding areas by, for example, conducting raccoon dog hunting. These areas include wetlands and lakes that were approximately 490 ± 1100 ha in size.

The camera traps were located in hunting areas that surround Helmi program wetlands. The hunting areas were on average 65 ± 45 km² in size. Study sites located around Finland, the most

northern location being in Tornio (Figure 2). In total there were 74 wetland locations and each location had a varying number of camera trap study sites ranging from one to 19 with one camera in each site. Cameras were placed in the hunting areas, which consisted of coniferous and mixed type forests and fields, and were supervised by local hunters. The exact location of each camera is not known, but the wetland area it was located in was recorded (Figure 2). As the hunting areas were large compared to the number of camera traps within the area it was assumed that the cameras were relatively far away and independent from each other. However, as we cannot verify this, the hunting area has been taken into account in the analysis.

Most cameras had attractants in front of the camera traps to lure the animals to the site. Attractants varied between a carcass, a trap that contained food and a feeder with grains or other provisions. In total, there were 232 camera traps that had an attractant in front of them and 120 camera traps with no attractants. Cameras containing no animal pictures were excluded from the dataset.

While the camera traps were active the whole year of 2024, we only observed pictures taken in 10-day periods in February-March as a representative subset, to limit the hours of work the picture watching took as they were watched manually. From each picture containing an animal, the animal was identified and the confidence of its recognition was marked down. Identifying animals was mostly clear, as the focal species of this study have different body types and have easily recognisable traits like tail size and length of legs and body (Figure 1). Out of all the sightings, less than one percent was not recognised.

The aim for watching the camera trap pictures was to mark down each picture of an animal of interest, but as it turned out to be too time-consuming another method was used for the bulk of the pictures. Following similar, previous studies (e.g., Selonen et al., 2022), animals captured within the same 30 minutes were considered to be the same individual. This means that the presence of animals was marked down in periods, where the start time was the first picture when the animal was seen and the end time was the last picture within the 30 minutes of the first picture. If different species were detected in the same pictures, the 30-minute period was ended with the arrival of the other species and continued afterwards with a new period up to 30-minutes. The same was done if more individuals of the same species arrived or left the site. Later the first dataset with the data of the sightings with all the pictures marked down was also changed to be periodical to fit with the other dataset.

The number of animals were counted if multiple animals of the same species were in the same picture. If individuals of different species were present at the same time, then they were marked down separately. The environmental information that was collected included the time of the picture (date and time), the habitat type (forest or field), and whether there was a visible attractant for the animals, for example a carcass or feeder with grains.

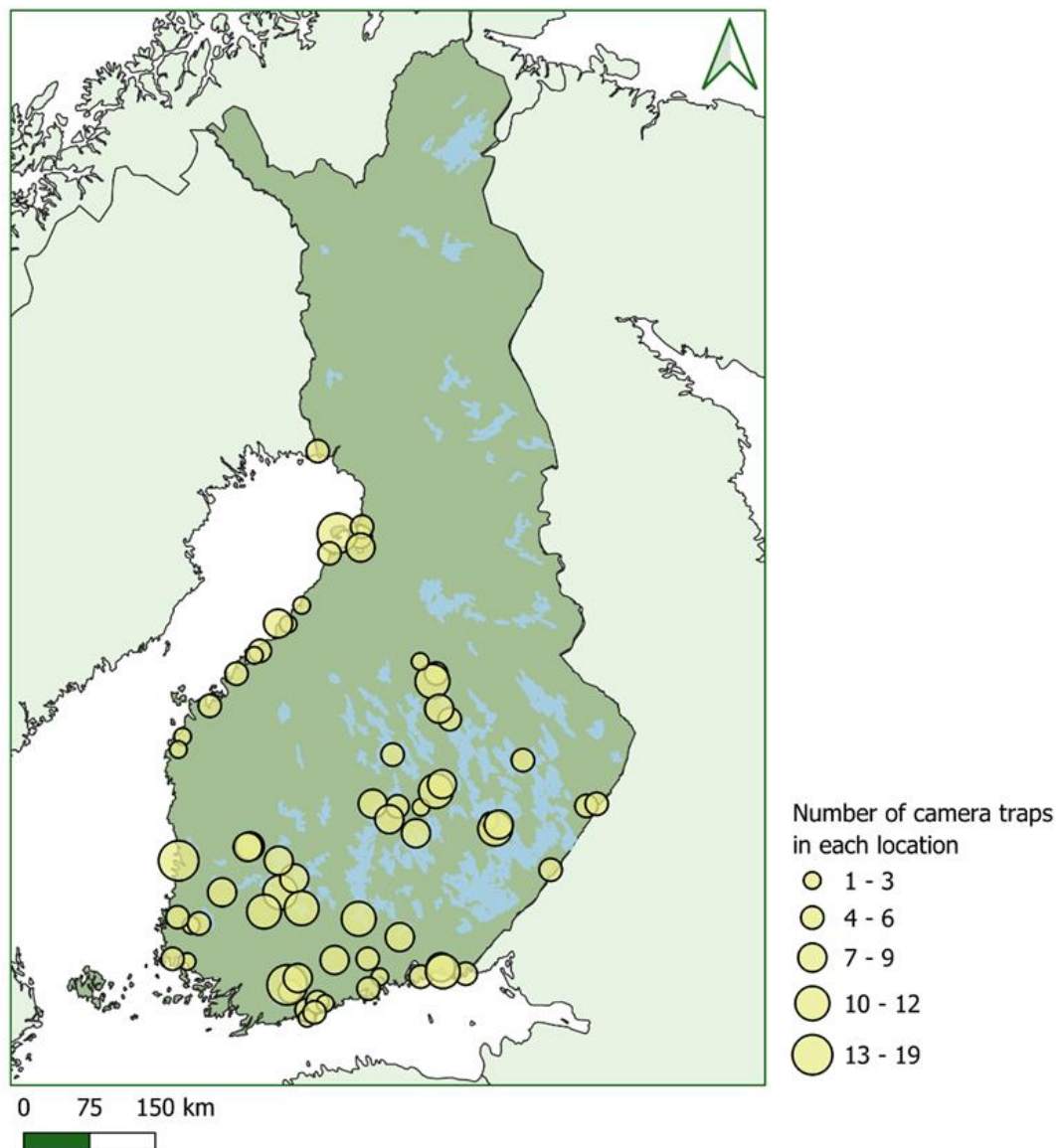


Figure 2. The locations of the camera traps and the number of cameras in each location. Source: Hallinnolliset aluejaot 1:10 000 (Vector) © National Land Survey of Finland, 2025, Ranta10 – Järvet (Vector, filtered to show lakes over 3 000 ha) © Finish Environment Institute, 2024, Base map: Admin 0 – Countries (vector, projection changed to ETRS TM35FIN -coordinates) © Natural earth, 2009.

2.3 Statistical analysis

Data processing and statistical analyses were conducted in RStudio version 4.5.1 (R core team, 2025). To improve the quality of the code used in statistical analyses OpenAI's (2025) ChatGPT was used. The plots and data formatting were done using packages ggplot2 (Wickham, 2016), dplyr (Wickham et al., 2023) and lubridate (Grolemund & Wickham, 2011). Package readxl (Wickham & Bryan, 2023) was used to import data.

2.3.1 Diel activity patterns of focal species

To inspect the temporal overlap of the focal species all the collected camera trap data was used to determine the diel activity patterns of the raccoon dog, the fox and the badger so that they could be compared to each other. As the dataset consists of camera trap pictures that have been taken in observation periods, the first picture from each period was used to indicate the activity of the animals found in the dataset. For example, when a period of pictures taken of a fox had its first picture taken at 23:15 and last picture at 23:27 the first picture was used to indicate the activity. Each of these detections was assigned to a decimal hour, ranging from 00:00 to 23:59, to portray the occurrence time within a 24-hour cycle.

Diel activity plots were made to have visual representation of the activity patterns of the species present in the dataset. The first created diel activity plot was made with all recorded species – the lynx, the fox, the raccoon dog, the badger, the pine marten, the wolverine and the wolf. The second and third diel plots include only the main three focal species of the study, the raccoon dog, the fox and the badger. In the second plot for each animal the activity was separated into sightings with and without an attractant. In the third diel activity plot, the activity patterns were further separated with the type of attractant that was present to see if the attractant type changes the pattern in diel activity in the focal species.

The significance of differences between activity patterns of the three mesopredator species were tested using pairwise Fisher's Exact Test. To differentiate day and night activity the 24-hour cycle was separated into two periods: day and night. Day was defined as the period between 6 am and 6 pm, whereas night was defined as the period from 6 pm to 6 am.

2.3.2 Time species spent in front of cameras

To determine the possible competition and temporal overlap the species might share, the time that the species spent in front of cameras was analysed using a generalised linear mixed model. This was done to recognise which species are using the potential resources most in the area.

The data used for the model was filtered to have only cameras where all three focal species were observed (n=16), excluding any cameras that recorded just one or two species. The time that species spent in front of a camera was calculated as the difference between the recorded start and end times of each observation and counted in minutes. If a sighting of a species consisted of only one image – meaning that the start and end times were identical – the time spent in front of the camera trap was determined to be one second.

The time the species spent in front of the cameras was set as a dependent variable in the used generalised linear mixed model and the species as an independent variable. In the model, the area around the wetland where cameras were located in and camera number nested within the area were treated as random effects. This was done because within one area multiple cameras were present and same animals could be recorded by different cameras. The models were made using Rstudio packages lme4 (Bates et al., 2015) for the analysis and lmerTest (Kuznetsova et al., 2017) to add p-values to the analysis and residuals were tested with the package DHARMA (Hartig, 2024).

To see whether the presence of other species affects the time a particular species spends in front of cameras, the mean time was calculated using only cameras where a single species was detected (cameras with raccoon dogs n=60, cameras with foxes n=68, cameras with badgers n=5). For example, the time foxes spent on average in front of cameras was calculated using only cameras that had no pictures of raccoon dogs or badgers in them.

2.3.3 Arrival times of the raccoon dog

To determine the effects the fox and the badger have on raccoon dogs' presence, the raccoon dog's activity patterns were examined more closely. This was done by inspecting raccoon dogs' arrival time to the camera location after 6 pm. The data was filtered to include only cameras with attractants (n=173), attractant being a carcass, a trap or a feeder, to have a common resource that attracted the species to the camera trap.

Each night in the dataset was assigned a unique ID to indicate the corresponding date. The arrival time of the first raccoon dog was measured in minutes starting from 6 pm. For each night, the total time raccoon dogs spent in front of the cameras and the number of raccoon dog sightings were also recorded. If there was only one picture taken, making the start and end time of the sighting to be the same, it was marked to be equal to one second and not as zero to indicate the presence of the species in the area. The presence or absence of the other focal species was also marked down and included in the analysis, with fox and badger presence counted when the detections occurred during nighttime (6 pm – 6 am).

As the camera trap data was recorded in the spring when the daytime lengthens fast, each day was given a running number to indicate the changing day lengths. Day of first camera trap pictures was numbered 1. and the second 2. and so on. In the analysis, the number of the day was used as a continuous variable to note the change in daylight hours.

The time in minutes it took for the raccoon to arrive after nightfall was the dependent variable that was inspected using a linear mixed model. The presence and absence of foxes and/or badgers was used as independent variables and the area and camera number within the area were used as random effects. The residuals were tested with the package DHARMA and the linear mixed model was done using package lme4. Additionally, the pairwise contrasts between foxes and badgers were checked using package emmeans (Lenth, 2025).

3 Results

3.1 Diel activity patterns of focal species

The significance of activity patterns between species was tested using all of the data and pairwise Fisher's exact test. The results showed significant differences between foxes and badgers ($X^2 = 27.65$, $p < 0.001$) and foxes and raccoon dogs ($X^2 = 181.22$, $p < 0.001$), but no difference between raccoon dogs and badgers ($X^2 = 0.016$, $p = 0.84$). This indicates that raccoon dogs and badgers have similar diel activity patterns whereas foxes' activity patterns differ from the other two species. The diel activity plots visualise the times of activity when the animals were captured in the camera traps. They show how raccoon dogs and badgers are strictly nocturnal and so have similar patterns whereas foxes are also active during the daylight hours making their diel activity different from that of raccoon dogs and badgers (Figure 3).

Raccoon dog was the most common animal to be captured in the camera traps, recorded 1,918 times (Figure 3). The second most common animal was the fox with total of 974 detections in the camera traps. Out of the three species this thesis focuses on, badger was the most elusive with 213 detections. While the data includes sightings of other species than raccoon dog, fox and badger, the number of observations of these other species, the lynx, the pine marten, the wolverine and the wolf, is considerably smaller than the number of focal species observations (Figure 3).

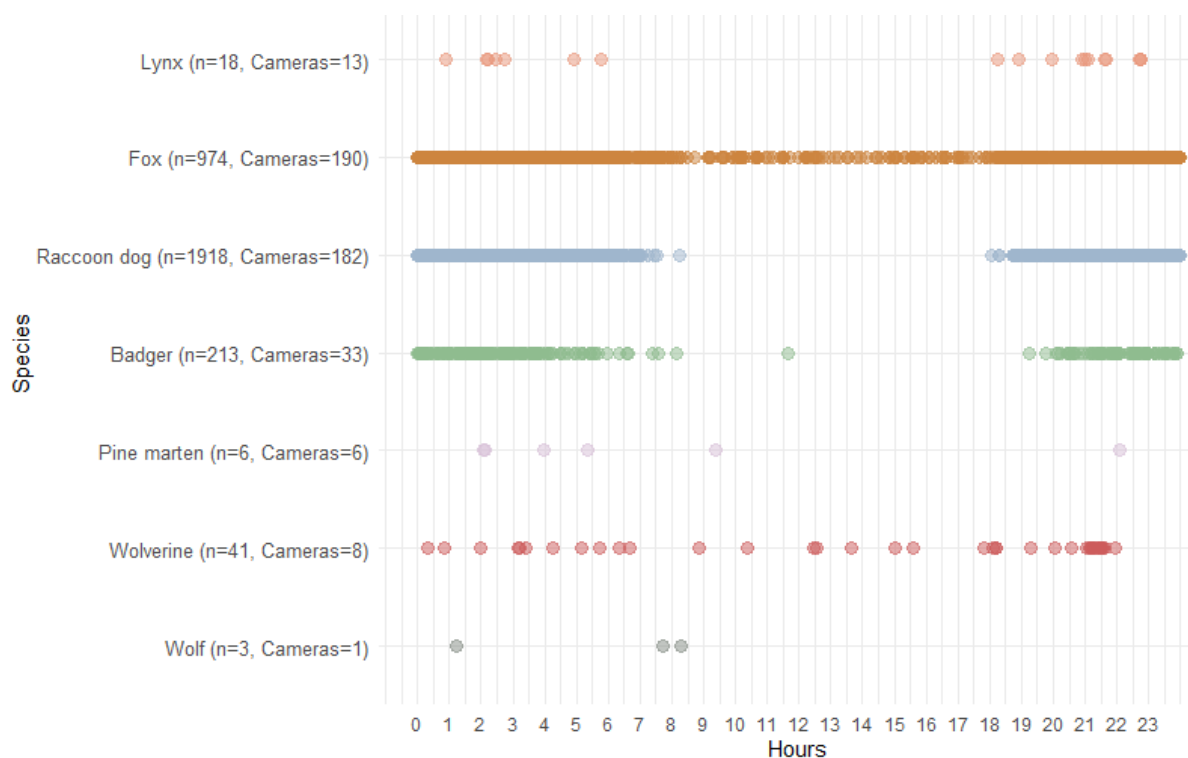


Figure 3. The diel activities of all species – the lynx, the fox, the raccoon dog, the badger, the pine marten, the wolverine and the wolf – that were detected from the camera trap pictures and the times when the activity was detected. The number of observations and the number of camera traps that captured pictures of each species can be seen inside brackets after the species name. The x-axis indicates the decimal hours of the day and the y-axis represents the included species.

In Figure 4, the activity of the focal species is observed with and without the attractants to see how food availability might affect the activity of the species. From the observations of the available data, it seems that raccoon dogs are rather strictly nocturnal with there being no sightings during the day between 09:00 and 18:00 (Figure 4). Similar pattern can be observed with the badger, as while there are less observations, they are mostly concentrated to the hours of morning, evening and night (Figure 4). This suggests that badgers are also mostly nocturnal. Foxes, however, do not seem to avoid daylight hours as strictly as the other two species as they have been captured in the camera traps around the clock. The activity is more heavily concentrated around the night hours but continues, nonetheless, around the clock (Figure 4).

In all the focal species, the presence of attractant does not seem to affect the timing of their activity. From cameras that had detected at least one of the focal species, the average of observed animals was 14.9 animal individuals in cameras with an attractant (n=181). In cameras without the attractant (n=79), the mean value of focal animal individual observations was 5.29.

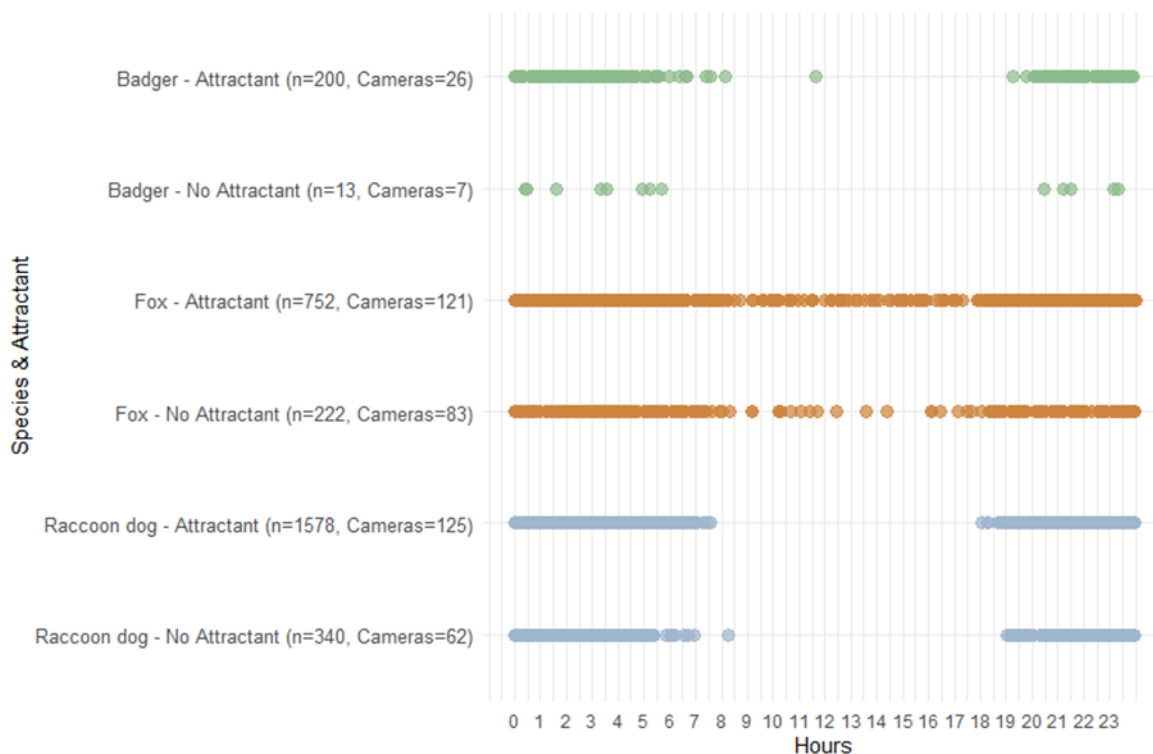


Figure 4. The diel activity of focal species, the raccoon dog, the fox and the badger, with and without the presence of an attractant. The number of camera traps that captured each species and the number of observations is shown in brackets after species name. The x-axis indicates the decimal hours of the day and the y-axis represents the included species.

The presence of an attractant was further separated into the different attractant types: carcass, trap with food and feeder with grains or other provisions (Figure 5) to see whether there is difference between the different attractant types and the diel activity of the focal species. The diel activity patterns do not seem to change depending on the attractant (Figure 5). Overall based on a descriptive summary, cameras with a feeder showed the highest mean number of sightings per camera per species (Supplement Table 1).

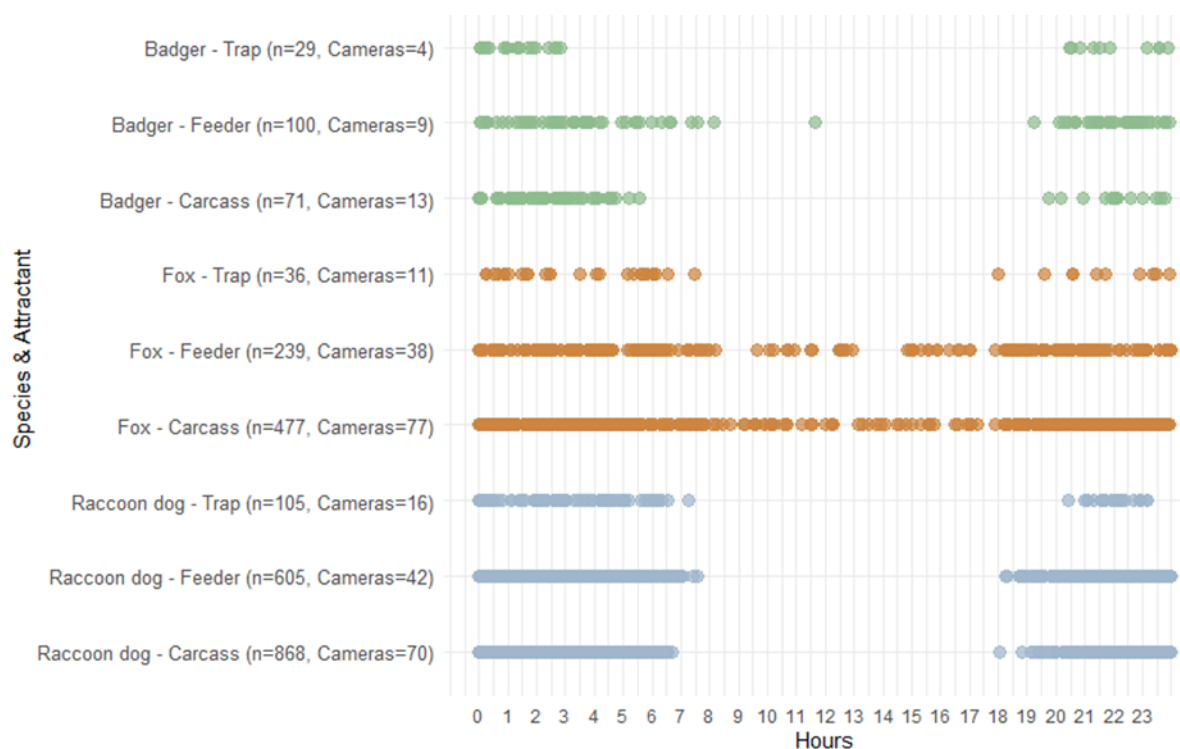


Figure 5. The diel activity of the focal species, the raccoon dog, the fox and the badger, only with attractants which are separated further to the different types of attractants used – trap, feeder and carcass. The number of sightings of each species with the different attractant types and the number of camera traps that captured the species is included in the plot. The x-axis indicates the decimal hours of the day and the y-axis represents the included species.

3.2 Time species spent in front of cameras

To see which species were prominent in cameras – and possibly also using the common resources the most – the time spent in front of cameras was analysed. The data that was used in this was filtered to only include pictures from cameras that had all three species – raccoon dogs, badgers and foxes – present. This resulted in 492 time periods where animals were captured in pictures. Out of those sightings 22 % were foxes, 46 % were raccoon dogs and 32 % were badgers. Cases where within one photo there were more than one species were rare (six pictures). Pictures with two or more individuals of the same species were more common with 76 pictures in total. 64 pictures had two or more raccoon dogs, five pictures had two foxes and seven pictures had captured two badgers.

Based on the results of the generalised linear mixed model, badgers were found to spend most time in front of the cameras (7.72 minutes) whereas foxes and raccoon dogs used less time. Foxes spent the least amount of time in front of the cameras (3.54 minutes) and raccoon dogs spent a bit more time (4.93 minutes) (Table 1).

Table 1. Results from the generalised linear mixed model analysing the time the focal species, the raccoon dog, the fox and the badger, spent in front of the camera traps. The time species spent in front of the cameras was used as the dependent variable and species as an independent variable. Area and camera number nested within the area were used as random effects. In the model only camera traps (n=16) that had captured all three focal species were used.

	Estimate (min)	Std. error	z-value	p-value
Intercept (Badger)	7.724	1.030	7.498	<0.001
Fox	-4.189	1.237	-3.387	0.001
Raccoon dog	-2.794	1.083	-2.580	0.010

The mean time animals spent in front of the cameras when no other focal species were present was also calculated. When raccoon dogs were alone, they spent on average 8.91 minutes in front of the cameras (observations n=509, cameras n=60). This is over three minutes more than what raccoon dogs spent when other species were present. Foxes spent 5.16 minutes (observations n=265, cameras n=68) in front of the cameras when other species were absent which is one minute more than when other species were present. However, badgers spent considerably less time in front of the cameras when alone, only 3.44 minutes, making it four minutes less than when other species were present. Possibly the low number of badger sightings (observations n=10, cameras n=5) affects the results and does not give the full picture.

3.3 The effect of fox and badger presence on the raccoon dog arrival times

In areas with only raccoon dogs the time it took the species to arrive after 6 pm was 445.1 minutes (approximately 01:25 AM) (Table 2). When foxes were present the time of arrival of raccoon dogs was 64.4 minutes sooner, making the time it took to arrive to the site after 6 pm to be 380.7 minutes (approximately 00:20 AM) (Table 2, Figure 6). While not being statistically significant the presence of badgers shows a similar effect – raccoon dogs arrived 27.5 minutes sooner in front of the cameras, making the arrival time after 6 pm to be 417.6 minutes (approximately 00:57 AM) when badgers were present. The presence of both foxes and badgers at the same sites also makes the raccoon dog arrive to the site 1.0 minute sooner but this is not statistically significant. Overall, the trend is that with other species present raccoon dogs arrive to the site sooner than when there are only raccoon dogs present. The contrasts that were tested can be found in the supplements (Supplement Table 2).

The day order was included in the model to see if the lengthening daylight hours would have an effect on the time taken for the raccoon dogs to arrive to the site. The negative estimate of -

3.1 minutes on average suggests that as the daytime lengthens raccoon dogs arrive to the site earlier (Table 2).

Table 2. The results of a linear mixed model used to estimate the time it took raccoon dogs to arrive in front of the camera after 6 pm. The time in minutes it took for the raccoon dog to arrive was used as the dependent variable and the presence and absence of foxes and/or badgers was used as independent variables. Area and the camera number nested within the area were used as random effects. In the model only the camera traps ($n=173$) that had an attractant were included in the model. Day order is included in the model to note the lengthening daylight hours in spring.

	Estimate (min)	Std. error	z-value	p-value
Intercept (Only raccoon dogs present)	445.067	24.433	18.216	<0.001
Foxes present	-64.388	13.790	-4.669	<0.001
Badgers present	-27.477	22.037	-1.247	0.212
Foxes and Badgers present	-0.956	40.072	-0.024	0.981
Day order	-3.055	1.464	-2.087	0.037

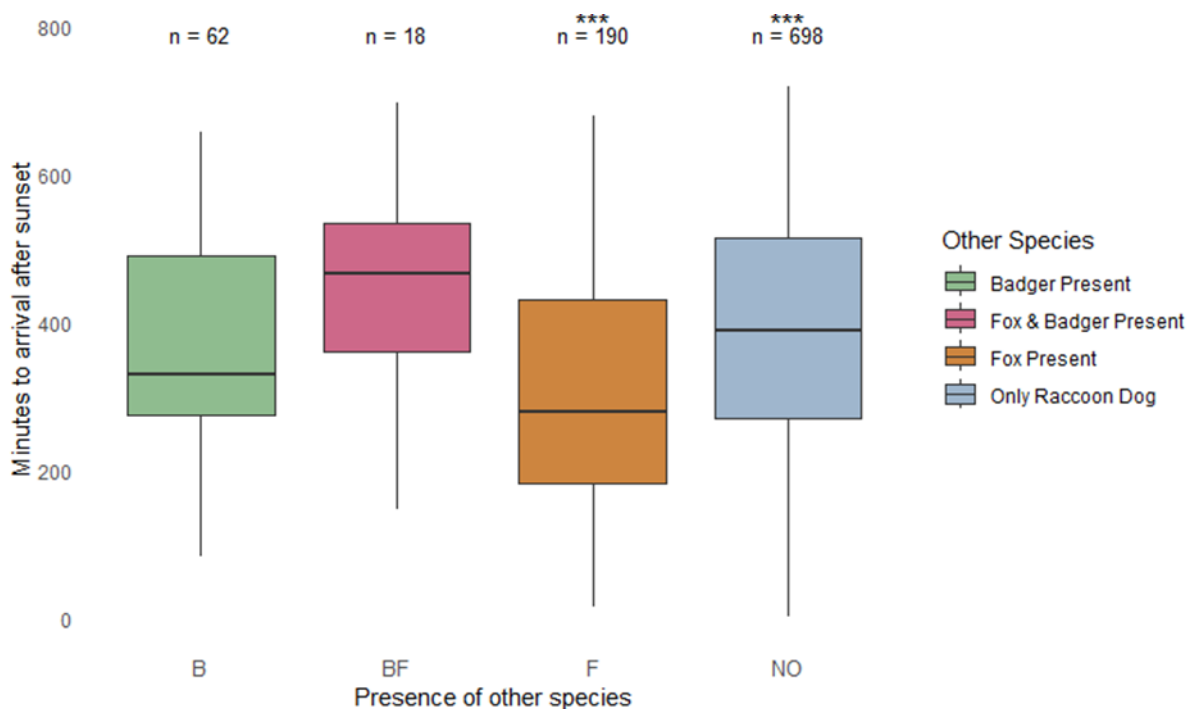


Figure 6. The minutes it took the raccoon dog to arrive in front of the cameras after nightfall (6 pm). Camera traps ($n=173$) used in this plot had an attractant in front of them. The presence of other focal species, the fox and the badger, is included in the model to see whether their presence affects the arrival times of raccoon dogs. The included number of observations marks the nights with raccoon dog presence that are grouped by the presence of other focal species.

4 Discussion

In my thesis, I studied the diel activity and possible temporal overlap between the native mesopredators, the badger and the fox, and an invasive alien mesopredator, the raccoon dog. Temporal overlap was studied using diel activity plots to visualise the activity of different species around the clock. Mostly the species were nocturnal, as I expected in my hypotheses, but foxes were also found to be active during the day.

Next, I explored which species spent the most time in front of the cameras and thus had the opportunity to also use most of the common resources. In the camera traps that had all three species present, badgers spent the longest time in front of the cameras.

Lastly, I studied the effect that the presence of native species, the fox and the badger, might have on the raccoon dog behaviour. The results suggest that with an attractant and foxes present, the raccoon dog changes its behaviour by arriving to the site sooner. This might indicate a competition between the species so that the raccoon dog becomes more active when a competitor, that is another mesopredator, is present.

4.1 Temporal patterns and attractant preferences of nocturnal mesopredators

The first aim in this thesis was to recognise the diel activity patterns of the focal species to see whether the species share the same times of activity. Based on the data available in this study, I find a temporal overlap between the three species as seen from the diel activity plots (Figures 3, 4 and 5). The results allow the rejection of the null hypothesis that the species' activity would be evenly distributed across the diel cycle and would not separate their activity to any specific time. Instead, the data indicates that all the focal species are mostly nocturnal. Previous studies support this by showing that raccoon dogs and badgers are primarily nocturnal (Kowalczyk et al., 2003; Monterroso et al., 2014; Schwemmer et al., 2021; Zoller & Drygala, 2013) and foxes, while being mostly nocturnal, are more flexible in their temporal activity (Ikeda et al., 2016; Monterroso et al., 2014).

Temporal niche segregation is important for carnivores to enable coexistence (Monterroso et al., 2014). While differences in activity times between badgers and raccoon dogs were not detected based on this study's data, foxes can be active during the daylight hours with a preference to nighttime as this and previous studies show (e.g. Monterroso et al., 2014). As the

fox shows flexibility in its activity patterns, the use of daylight hours can be a way to avoid competition with the other nocturnal mesopredators, such as the badger and the raccoon dog.

As seen in the diel activity plots (Figure 4 and 5), the presence of attractant food does not appear to alter the activity patterns of the focal species, although foxes may exhibit slightly increased daytime activity when attractants are present. However, this cannot be confirmed due to the smaller sample size in cameras without an attractant and the lack of statistical testing.

Due to the smaller sample size in cameras without an attractant and the lack of statistical testing, no firm conclusions can be drawn about the effects of attractant type on species activity. Nevertheless, some descriptive patterns in camera trap detections were observed. Most fox and raccoon dog detections occurred at camera traps with carcasses, whereas badgers were recorded more frequently at sites with a feeder as an attractant (Figure 5). Badgers had a lot less sightings overall compared to the other two species, and therefore chance can affect the distribution of sightings of badgers. When mean numbers of detections per camera were calculated across the entire dataset, feeder sites showed the highest values for all focal species (Supplementary Table 1). These patterns are interesting but are only presented descriptively and are not tested in the current study and hence one can only speculate about their meaning. More research needs to be done to understand if there are any species-specific dietary preferences structuring the mesopredator community.

The attractant preferences of the species could be studied closer if ever a need rises to focus on a certain species and to attract individuals of that specific species. Previous studies conducting camera trap surveys have revealed that predator species do prefer different attractants (e.g. Avrin et al., 2021) and the level of decay can affect the species distribution (Avrin et al., 2021; Mills et al., 2019). While the use of attractants and camera traps in research is growing in popularity, the side effects should not be forgotten. For example, Meek et al. (2016) found that light and sound from camera traps can change the behaviour of animals.

Whilst attractants can considerably increase the likelihood of detecting the study species at the camera trap sites (Randler et al., 2020), their underlying activity patterns are shaped by ecological and environmental factors beyond just food availability. One important limitation of this study is that the data used here was only collected in spring, which prevents examination of seasonal changes in activity. Previous study suggest that species can change their times of activity in different seasons while still keeping the main characteristic of their activity times (Ikeda et al., 2016). In addition to seasonality, human disturbance is another factor that can alter

animal activity, often driving species to become more nocturnal (Gaynor et al., 2018). For example, Lovell et al. (2022) observed that foxes can become more nocturnal in areas where human disturbance is high. As in this study the areas that the camera traps were placed were used as hunting ground for raccoon dogs it could have impacted the diel activity of the species, as hunting and human presence in general can alter the species to become more nocturnal (Gaynor et al., 2018). Badgers have also been found to decrease time spent foraging and visits to food patches, delaying initiation for foraging and increasing vigilance when hearing sounds made by humans (Clinchy et al., 2016). The fear that human presence possibly caused to the focal species could have affected the behaviour of the species in both resource use as well as in their diel activity. However, neither seasonal variation nor human impact can be addressed with the present dataset.

4.2 Badger spent most time in front of cameras when all species co-occurred

The second aim in this thesis focused on the time each focal species spent in front of the camera traps. The results allow to abandon the null hypotheses and as hypothesized in the aims of the study the badger was seen to spend the most time in front of the camera traps compared to the other two mesopredators. Using cameras that had all three species present badgers spent on average almost eight minutes, raccoon dogs spent a little under 5 minutes and foxes spent less than 4 minutes in front of the camera traps.

The time usage can be explained by the bigger size and relative aggressiveness of badgers, so that they can dominate the common resources that were present at most camera trap locations. Previous studies have demonstrated that bigger species can deter other species away from the common resources (Barrull et al., 2014; Macdonald et al., 2004). In a study by Macdonald et al. (2004), conclusions were that badgers dominated over foxes and restricted their access to the baits provided by researchers. Furthermore, a prior detection of badgers at a site delayed fox arrival compared to times when the larger competitor was absent (Barrull et al., 2014). Similar effects can be seen from this study as when all three species were present the badger, being the biggest of the three species, spent the most time in front of the cameras while the other two spent less time.

Raccoon dogs were most abundantly sighted ($n=220$) from cameras with all three species present with badgers being second most abundant ($n=166$) and foxes the least common ($n=125$). In a previous study by Selonen et al. (2024a) out of the three focal species, the raccoon dog was found to have the highest density. Another earlier study recorded raccoon dogs to have been

the most common from the three species (Kauhala, 2007). This corresponds to the detections in this study as overall sightings of raccoon dogs were most common, with a total of 1918 sightings (Figure 3). This observed pattern, presumably affected by population density, could be influenced by behavioural factors such as avoidance and interference competition. Potentially the presence of other two mesopredators could deter fox from the site, as it is the smallest of the three focal species and may avoid areas dominated by larger competitors which has been previously demonstrated by Barrull et al. (2014). Additionally, the presence of attractants at the camera trap sites may have disproportionately drawn raccoon dogs, further increasing their detection compared to foxes.

When examining species activity at camera sites where no other focal species were detected, raccoon dogs spent on average over 8 minutes in front of the cameras. Foxes spent slightly more than 5 minutes on average, which seems similar to the time they spent when other focal species were present. Badgers spent less than 4 minutes on average when alone at a camera site. The relatively low number of badger detections overall can affect the time, especially compared to the overall higher number of sightings of raccoon dogs and foxes (Figure 3). Moreover, the badger observations were concentrated at camera trap sites equipped with attractants (Figure 4). Nearly all cameras where all three species were recorded had some form of attractant, increasing the likelihood of multiple species visiting the same site (Mills et al., 2019). Therefore, cameras that would detect badgers in the absence of foxes and raccoon dogs were rare, as the probability of multi-species visits rises with the presence of attractants (Mills et al., 2019).

4.3 Raccoon dog arrives sooner when other species are present

The third aim in this thesis was about testing the effects that the fox and the badger might have on the raccoon dog arrival times. When there were no other species than raccoon dogs seen in the camera traps, the arrival time was 1:25 AM (445 minutes after 6 pm). However, when other species were present in the area raccoon dogs arrived sooner to the site. Most noticeable is that when foxes were present, raccoon dogs arrived at the site over an hour – 64 minutes – earlier at 00:20 AM (Table 2 and Figure 6).

The results from this study indicate that raccoon dogs change their behaviour when other mesopredators are present in the area. Ability to change patterns in behaviour have been reported previously in varying contexts, for example when it comes to selecting habitats and nesting sites; when badger sets have higher number of badgers using them, other mesopredators

avoid these setts (Tammeleht & Kuuspu, 2018). Although species generally adhere to their preferred times of activity, they may exhibit temporal plasticity by adjusting activity times to reduce interspecific competition and facilitate coexistence (Monterroso et al., 2014). Linking back to the previously discussed point, where foxes were seen to have longer time intervals between occurrences when badgers were present – showing flexibility in behaviour to avoid interaction (Barrull et al., 2014).

The only statistically significant change in raccoon dog's arrival time was associated with fox presence. This may suggest that in relation to foxes, raccoon dogs do not avoid foxes spatially and instead alter their timing of the use of the site. While earlier arrival could indicate an attempt to secure access to the site of shared resource before foxes arrive, it can also represent temporal avoidance to reduce the probability of direct interactions. But given the small size difference between foxes and raccoon dogs, interpreting this behaviour as dominance should be done carefully. In either case the earlier arrival time of raccoon dogs is contrary to the presented hypothesis about the behaviour of raccoon dogs, as they do not delay their arrival when other species are present but advance the time they arrive.

The presence of badgers at camera trap sites did not have statistically significant effect on the raccoon dog arrival times, although raccoon dogs tended to arrive 27 minutes sooner when badgers were present. If raccoon dogs were actively avoiding badgers a stronger temporal shift might be expected as badgers are larger and may pose a greater threat to the smaller raccoon dog. Indeed, badgers are known to kill raccoon dog cubs that occupy badger setts (Kowalczyk et al., 2008), suggesting a potentially competitive or antagonistic relationship between the two species. Foxes and raccoon dogs also have been found to avoid cohabiting badger setts that have more than two adult badgers already present (Nowakowski et al., 2020). This indicates that both species avoid encounters with badgers.

Overall, the results show that raccoon dogs do continue to visit the camera traps sites regardless of the presence of other mesopredators. This possibly indicates a lack of spatial avoidance, as raccoon dogs do not avoid the sites where other mesopredators were recorded but arrived sooner to the site. This temporal shift could be a sign of temporal avoidance if the earlier arrival reduces the risk of a direct encounter while still allowing access to the common resource. However, it may also represent a form of competitive advantage as the raccoon dog tries to secure the food resource before other competitors. But overall, based on this study, it is difficult to know whether the earlier arrival of the raccoon dogs is an act of dominance or avoidance, or a

combination of both. The behavioural response of the raccoon dog is likely affected by multiple factors such as the identity of the other species and the nature of the interaction. Further research would be needed to be able to say confidently how the behaviour of the raccoon dog changes.

4.4 Changing daylight hours

The lengthening daylight time in spring was taken into account when making the analysis on raccoon dog arrival time. The results showed that as the days lengthen raccoon dogs arrive approximately 3 minutes sooner to the camera trap sites (Table 2). As days pass, the time raccoon dogs arrive to the camera trap locations becomes earlier, the time cumulates and thus follows the lengthening daylight hours: around February and March daylength grows approximately 3 minutes in the evening and 3 minutes in the morning. This indicates that raccoon dogs change their behaviour regarding to the daylight hours.

Similar changes have been recorded previously for example by Zoller and Drygala (2013) who found that as the daylight hours increase, activity of raccoon dogs also increases during daytime, since nights during summer (in central and northern Europe) are short and would not leave enough time to hunt and forage. As spring progresses the warming temperatures and rearing of pups might also increase raccoon dog activity overall.

4.5 Conclusions

The raccoon dog has been designated as a harmful invasive alien species in the EU (European Commission, 2017). Although member states and landowners are not obliged to reduce raccoon dog populations, efforts have nonetheless been made to limit its spread, particularly in areas where the risk to biodiversity is greatest, such as wetlands and important bird habitats in archipelagos. Such measures were also taken in the wetland project under Helmi programme, which also provided the data for this study. In Finland, hunters are encouraged to trap raccoon dogs and American minks to protect biodiversity (Suomen Riistakeskus, 2025; Vieraspeto.Fi, 2021). Yet, complete eradication of the raccoon dog seems impossible and thus the species will likely remain as a part of Finnish wildlife.

As raccoon dog populations in Finland have been observed to increase, fox populations have declined (Selonen, et al., 2024b). It is unclear whether raccoon dogs are the reason for the fox population declines and therefore the interactions between the two species should continue to be studied carefully. Whilst other aspects such as prey abundance, climate change and forest

management can also be reasons behind the decline of fox populations, raccoon dog presence should not be excluded from the list of possible reasons.

Knowledge on badger population in Finland could benefit from new surveying, but while the population density is by its nature, low (Kauhala & Holmala, 2011), the population itself has been found to grow and not to be affected by the spreading of raccoon dogs (Kauhala, 1995; Kauhala & Auttila, 2010). Previous studies have been conflicting, finding both no or little evidence of competition between raccoon dogs and badgers (e.g. Elmeros et al., 2018; Kauhala & Auttila, 2010; Nowakowski et al., 2020) or connecting the spread of raccoon dogs to local population declines in badgers (Rotenko & Sidorovich, 2017). As no clear signs of competition have been identified it remains unclear whether raccoon dogs have direct negative effects to badgers. However, as the species do share many resources, such as similar diets (Elmeros et al., 2018) and nesting spots (Kowalczyk et al., 2008), the interactions between species are unavoidable.

The results from this study suggest raccoon dogs might be able to change their behaviour, according to the other species present in the same area. This is a competitive advantage as the presence of foxes prompted raccoon dogs to arrive sooner to the site of a common resource. While this study highlights the behavioural flexibility of raccoon dogs, further research is needed to be sure of the temporal interactions and behaviours of the focal species, preferably with a bigger number of observations captured and in different seasons.

Overall, the study of invasive species should not be taken lightly, especially in the time where warming climate and rise in global trade allows more species to spread and settle in new regions. In Finland, the milder winters might allow raccoon dogs to increase populations and widen their habitats to more northern parts of the country (Kauhala, 2007). As the raccoon dog is already the most common out of the three focal species (Kauhala, 2007) its widening range could cause more pressure to native species and increase competition between the raccoon dog and the native mesopredators.

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Supplements

Table 1. The mean of sightings of each of the focal species, the badger, the fox and the raccoon dog, with each type of attractant used. Mean sightings/camera shows the average number of sightings of each species with the different attractant types. Number of cameras shows how many cameras captured the species.

Attractant type	Species	Mean sightings/camera	Number of cameras
Carcass	Badger	5.46	13
Feeder	Badger	11.1	9
Trap	Badger	1.86	7
No attractant	Badger	7.25	4
Carcass	Fox	6.19	77
Feeder	Fox	6.29	38
Trap	Fox	2.67	83
No attractant	Fox	3.27	11
Carcass	Raccoon dog	12.4	70
Feeder	Raccoon dog	14.4	42
Trap	Raccoon dog	6.56	62
No attractant	Raccoon dog	5.48	16

Table 2. The contrasts from the linear mixed model that was used to estimate the time it took raccoon dogs to arrive in front of the cameras after 6 pm. The contrasts compare the arrival time of raccoon dogs when they are detected alone with the arrival times of raccoon dogs when other species are present. Fox vs Badger compares the arrival time of raccoon dogs when foxes are present to the arrival time of raccoon dogs when badgers are present.

Contrast	Estimate	SE	Z-value	p-value
Fox present vs only Raccoon dogs present	-64.388	13.8	-4.669	<0.0001
Badger present vs only Raccoon dogs present	-27.477	22.0	-1.247	0.850
Both Badger and Fox present vs only Raccoon dogs present	-0.956	40.1	-0.024	1.000
Fox present vs badger present	-36.911	24.2	-1.524	0.510