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Do the behavioural patterns of beavers reflect the re-occurence of wolves?

Diploma thesis

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In Prague, 28.03.2024 Micol Genazzi

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Abstract

After facing extinction in the late 19th century, the Eurasian beaver (*Castor fiber* L.) has recently repopulated the Czech Republic. Belong to the beavers, another animal has recently reappeared in the park: the wolf (*Canis lupus*, L.).

This study aims to understand how the reoccurrence of wolves in the Šumava National Park has potentially induced changes in the circadian rhythms of beavers. To achieve this, a basic dataset was obtained by monitoring selected individuals between the years 2022–2024 in the Šumava NP. The telemetry was especially focused on the start and end of the activity of the animal. These data were compared with data collected more than a decade ago, between 2008 and 2012. Analyses were carried out at the annual and seasonal scales by using the program R with the overlap package.

Primary data collection for the study spanned from October to June 2022/23, monitoring 7 beavers across 5 territories. Secondary data collection took place from October to March 2023/24, observing 8 beavers across 6 territories. The results showed a coefficient of overlap (Δ_4) of 0.85 indicating a high degree of similarity between the two datasets and a 95% confidence interval ranging from 0.82 to 0.88. The resulting graphs show a similar start of activity between the two periods, but a different end of activity.

The study showed that beavers prefer mostly nocturnal behaviour. Research suggests that recent beavers have changed their circadian rhythm, showing an earlier start and end of activity, possibly due to the reoccurrence of wolves.

Keywords: telemetry, circadian rhythms, prey-predator interactions, Šumava National Park

Abstrakt

Bobr evropský (*Castor fiber* L.), kterému koncem 19. století hrozilo vyhynutí, nedávno znovu osídlil Českou republiku. K bobrům přibyl i další živočich, který se v území nedávno znovu objevil: vlk (*Canis lupus*, L.).

Cílem této studie bylo pochopit, zda opětovný výskyt vlků v Národním parku Šumava potenciálně vyvolal změny v cirkadiánních rytmech bobrů. Za tímto účelem byl získán základní soubor dat sledováním vybraných jedinců v letech 2022-2024 v NP Šumava. Telemetrie byla zaměřena zejména na začátek a konec aktivity zvířete. Tyto údaje byly porovnány s daty získanými před více než deseti lety, v letech 2008-2012. Analýzy byly provedeny v ročním a sezónním měřítku pomocí programu R s balíčkem overlap.

První etapa sběru dat pro studii probíhala od října do června 2022/23 a sledovalo se 7 bobrů v 5 teritoriích. Druhá etapa sběru dat probíhala od října do března 2023/24, kdy bylo pozorováno 8 bobrů v 6 teritoriích. Výsledky ukázaly koeficient překryvu (Δ_4) ve výši 0,85, což naznačuje vysokou míru podobnosti mezi oběma soubory dat a 95% interval spolehlivosti v rozmezí 0,82 až 0,88. Výsledné grafy ukazují podobný začátek aktivity mezi oběma obdobími, ale odlišný konec jejich aktivity.

Studie ukázala, že bobři preferují aktivitu v noci. Výzkum naznačuje, že v poslední době bobři změnili svůj cirkadiánní rytmus, který vykazuje dřívější začátek a konec aktivity.

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1. Introduction

The reoccurrence of the wolf in certain territories within the Czech Republic has revived interest in understanding the intricate dynamics between predators and prey species, especially their effects on the ecosystem and prey behaviour. Among the wild species affected, the Eurasian beaver (*Castor fiber* LINNAEUS, 1758) stands as a key player, whose role and behaviour are deeply intertwined with the ecological structure of its habitat.

Despite being recognized as a keystone species, the behaviour of the European beaver in terms of activity patterns over time and space is still poorly understood. While numerous studies have been done on topics like food preferences, habitat selection, and territoriality, it has always been challenging to understand the subtleties of individual beaver behaviour. The nocturnal, semi-aquatic and naturally shy nature of the beaver limits direct observations, requiring arduous methods to fully understand its behaviour.

In this pursuit, telemetry emerged as a crucial tool, albeit with its own set of challenges. Although it provides ongoing records of individual movements, telemetry requires significant time investment, specialized technical equipment, and skilled observers. However, the ability to study changes in beavers' behaviour over time has provided the opportunity to reveal previously hidden aspects of their lives.

In the present work, I have attempted to record the activity of beavers and any changes in their circadian cycle, to deduce their causes and consequences and to reveal any relations with the return of the wolf (*Canis lupus*, L.) to the territory.

Finally, based on the results obtained, I derived the beavers' circadian cycle models and compared them with the models of 10 years ago, in order to try to understand whether behavioural differences have occurred since the return of the wolf to the area.

2. Literature review

2.1 The effects of predator on prey

In the intricate web of nature, predators exert a profound influence on prey species, shaping their behaviour, populations and evolutionary adaptations across various ecosystems (Orrock et al., 2010). The delicate interplay between predators and prey takes place through a wide range of interactions, from direct predation to indirect effects (Orrock et al., 2010).

Acting as natural regulators, predators play an important role in controlling prey populations, suppressing uncontrolled growth, and reducing resource depletion (Nelson et al., 2004; Peacor, 2002). In response to these pressures and the fear of predation, prey species evolve an arsenal of adaptive measures, developing complex behaviours such as camouflage, hypervigilance, and defensive mechanisms, improving their evasion tactics against predators over generations (Peacor, 2002; Randler, 2006).

Firstly, predators act as regulators of prey populations, preventing overpopulation and subsequent resource depletion within ecosystems, which is critical to maintaining ecological balance and sustainable resource utilisation (Nelson et al., 2004; Peacor, 2002). In addition, the ramifications of changes in prey populations due to predation reverberate throughout the ecosystem, potentially impacting populations of other species within the intricate food web (Nelson et al., 2004; Orrock et al., 2010). These fluctuations often lead to cascading effects, reshaping community structures and altering the dynamics of entire ecosystems (Orrock et al., 2010).

Secondly, the presence of predators induces significant shifts in how prey forage and utilize habitats. Prey species adapt their behaviours to minimize predation risks, resulting in consequential alterations in feeding patterns and habitat selection (Randler & Kalb, 2020). These changes brought about by continuous interactions with predators drive the evolution of prey species, promoting traits that improve survival against predators (Peacor, 2002). These adaptive changes may consist of changing the timing, location or manner in which they seek food or shelter to minimise the risk of predation, influencing the distribution and availability of resources within ecosystems (Randler & Kalb, 2020).

For example, in a study carried out by Randler & Kalb (2020) investigating how both nocturnal and diurnal rodents avoid predators, it was found that there's a balance between the risk of being preyed upon and the act of searching for food. This balance seems to lean more towards avoiding predators rather than prioritizing feeding on a rich food supply (Randler & Kalb, 2020), leading in extreme cases to the complete interruption of actual feeding behaviour (Randler, 2006). However is interesting to observe that when the animals are aware of the food source and food quality, they may trade-off the foraging against the risk of predation (Randler & Kalb, 2020).

Moreover, the impact of predators extends beyond immediate physical encounters, showcasing the phenomenon of remote predator effects (Orrock et al., 2010). Predators in one area can significantly influence prey behaviours in seemingly predator-free spaces. This transmission of predator cues highlights the interconnectedness of ecosystems, emphasizing the far-reaching implications of predator presence on prey populations across spatial distances (Orrock et al., 2010). Apart from behavioural adaptations, the influence of predation extends deeply into the physiological responses of prey species. The continual presence of predatory threats induces stress responses within prey populations, potentially affecting growth rates, reproductive success, hormonal balance, and overall population health (Apfelbach et al., 2005). This stress could lead to resource allocation changes within prey, moulding their physiological functions to prioritize survival needs (Apfelbach et al., 2005).

2.1.1 Effects of the wolf on beaver

Wolves and beavers are keystone species in numerous ecosystems, influencing biodiversity, habitat structure, and ecosystem function. Among the many predator-prey dynamics, the ecological relationship between these two species stands as an intriguing case study, where predation by wolves impacts the behaviour and population dynamics of beavers.

The interplay between wolves and beavers within ecosystems extends beyond mere predator-prey dynamics, encompassing intricate behavioural adaptations and ecological implications. Research conducted by Gable et al. (2018) in their study on wolf predation rates on beavers sheds light on the direct impact wolves have on beaver populations. The presence of wolves as apex predators significantly influences herbivore populations such as deer and elk, indirectly affecting beavers (Gable, 2021). In fact, by regulating herbivore populations, wolves indirectly influence the browsing pressure on trees and shrubs, subsequently altering the vegetation along riverbanks—an essential factor for beavers' dam-building and lodge-construction needs (Gable et al., 2023). This herbivore-induced alteration in vegetation availability has a substantial impact on the habitat and available resources for Eurasian beavers, influencing their foraging responses to predator odours and showcasing their adaptability in mitigating potential risks associated with the presence of predators in their environment (Rosell & Czech, 2000).

The presence of wolves prompts behavioural adjustments in beavers, as observed by Severud et al. (2011), where predator cues led to reduced use of foraging trails by North American beavers. Studies, such as those by Rosell & Sanda (2006), highlight how predators, including wolves, influence beaver scent-marking behaviour, demonstrating the intricacies of behavioural adaptations in response to perceived predation risks. A study conducted by Gable et al. (2018) underscores how beavers adapt their behaviours when confronted with the risk of wolf predation. These adaptations could involve changes in their dam-building patterns, favouring smaller structures or opting for locations providing increased cover (Basey & Jenkins, 1995). Moreover, in areas where wolves are prevalent, beavers exhibit further behavioural adaptations. They might prioritize building dams in concealed locations, demonstrating their adaptability to mitigate potential risks associated with increased exposure to predators (Gable et al., 2016; Gable & Windels, 2018).

2.2 The return of the beaver in the Czech Republic

The Eurasian beaver is a native species in the Czech Republic. During the 18th to 19th centuries, it faced widespread extermination across much of its range in Europe (Mikulka et al., 2022b). This extermination led to a significant reduction in their population across many parts of the continent. It faced extermination primarily because of the harm it caused and also due to the hunting for its castoreum, meat, and fur (Mikulka et al., 2022a) as well as the loss of habitats (Máca et al., 2015).

The recent resurgence of the beaver population began in the 1970s (Vorel et al., 2017) when the first beavers repopulated the Czech Republic by migrating along the Morava River from Austria, where the beaver was reintroduced (Mikulka et al., 2022a). Beavers have also migrated into the Czech Republic along the Elbe River from Germany in 1992 (Halley et al., 2021). Additionally, reintroduction efforts were undertaken during the 1990s, introducing beavers into various other locations within the Czech Republic (Mikulka et al., 2022a). From around 50 individuals in 1990, the count surged to an estimated 15,000 individuals by 2023 (Berg, 2023; Mikulka et al., 2022a).

2.2.1 Distribution and habitat

Beavers are classified into two main species: the Eurasian beaver, found across Siberia, Mongolia, and nearly all of Europe except for Mediterranean regions; and the North American beaver (*Castor canadensis* Kuhl, 1820), prevalent in Canada, Alaska, most parts of the United States, and also present in Chile and Argentina (Treves et al., 2020).

In the Czech Republic there are approximately 15,000 Eurasian beavers as of 2023 (Berg, 2023). The highest concentration of beavers in terms of population is in the Pilsen region, followed by South Moravia (Berg, 2023). Currently, beavers are extensively distributed in Moravia and appear to be approaching full capacity within the Morava watershed (Figure 1), which covers the majority of the region (Halley et al., 2021). From the Morava River basin they have expanded into regions in Silesia, western and southwestern Bohemia, and even into previously unpopulated areas in South, East, and Central Bohemia (Vorel et al., 2017). Their presence is notable along major watercourses such as the Morava and Elbe rivers and their tributaries, marking a significant resurgence in their distribution throughout the country (Vorel et al., 2017).

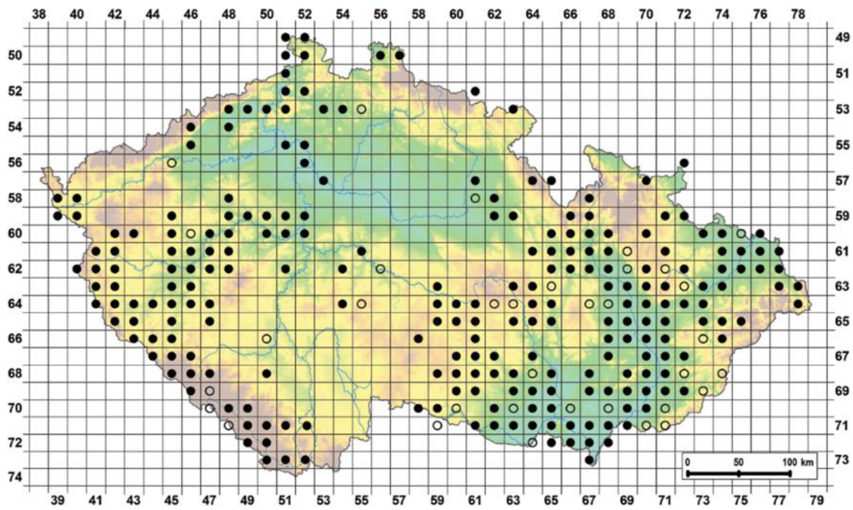

Figure 1: Current distribution of the Eurasian beaver in the Czech Republic – status up to end of 2015, solid circles marking permanent occupation of the square, empty circles marking temporary settlement (Source: Vorel and Šafář, unpubl.)

Typical features of beaver habitats include riparian zones, wetlands, and areas along primary watercourses in foothills and plains (Treves et al., 2020). They occupy various environments, including intermittent-flow streams, standing water in lakes or ponds, and bogs without open water (Baker & Hill, 2003). Moreover, they are often found in floodplain forests near medium to large rivers (Vorel et al., 2008), alongside shallow marshes, seasonally flooded meadows, and wet areas with deciduous shrubs. The presence of tall trees and bushes is crucial in these beaver-inhabited sites (Fustec et al., 2003).

Beavers in the Czech Republic favour areas with gentle slopes, calm surfaces, and devoid of large boulders (Mikulka et al., 2022a). Regarding the climate condition, altitude is an indirect limitation as higher altitudes (above 900 meters) reduce the beaver's food supply (Vorel et al., 2008). Beavers have the ability to form colonies in urban settings, but they tend to utilize this habitat type more frequently when population density is high. However, as human impact increases, the availability of suitable sites for beaver lodges decreases (Pachinger & Hulik, 1999).

2.2.2 Food preferences

The feeding behaviour of the beaver is that of a strict herbivore, with a broad dietary range that follows a seasonal pattern. Considered opportunistic generalist herbivores, beavers possess the capability to consume a variety of plant species based on availability (Vorel et al., 2015). Both the Eurasian and North American beavers employ an opportunistic foraging strategy, consuming various woody plant species depending on local accessibility within their immediate environment (Vorel et al., 2015). This flexible behaviour enables them to adapt their diet to the availability of their surroundings.

From spring to autumn, the beaver primarily consumes green vegetation found abundantly along the banks of watercourses (Mikulka et al., 2022b). While in winter, the beaver utilizes its impressive ability to cut down woody plants employing their sharp incisors, relying on the inner bark (bast) and young bark as its primary source of food during the colder months (Krojerová-Prokešová et al., 2010). Beavers demonstrate a broad range of tree-cutting behaviours, encompassing various sizes and types of trees, from small softwoods less than 2.5cm (1 in) in diameter at breast height (DBH) to large hardwoods measuring up to 1.8 m (6 ft) in DBH, with occasional instances of girdling larger trees without complete felling (Taylor et al., 2017).

In some regions, beavers commonly consume birch (*Betula L.* spp.) (Figure 2) or alder (*Alnus L.* spp.), while in areas with a broader variety of plant species, they tend to show a preference for willow (*Salix L.* spp.) (Figure 2) and poplar (*Populus L.* spp.). In the Czech Republic, beavers demonstrate a clear preference for willows and poplars as their primary food sources (Vorel et al., 2015). These two tree species collectively account for up to an average of 80% of the beavers' diet in terms of volume. (Mikulka et al., 2022b). The preference for willow and poplar among beavers may stem from several factors. These species might be favoured due to their digestibility, nutrient content, and potentially because the bark is easier to separate from the wood compared to other tree species (Mikulka et al., 2022b).

Figure 2: fresh willow (on the left) and birch (on the right) cuttings by beavers (Taylor et al., 2017)

2.2.3 Behaviour and spatial patterns

Beavers, as semiaquatic rodents, are renowned for their remarkable behaviours that shape their habitats and ecosystems (Anderson & Rosemond, 2007). They exhibit extraordinary engineering skills by constructing dams across waterways using branches, logs, and mud, creating ponds and altering landscapes, providing protection and fostering wetland habitats (Gaywood, 2018). They are territorial rodents, living in colonies (families) and communicating through various vocalizations and tail slaps to mark territories and warn of danger (Ciechanowski et al., 2011). A typical family consists of a monogamous adult pair, young of the year, yearlings and sometimes two-year-olds or older (Rosell & Czech, 2000). Territory defence is aided by the smell marking of the territories with castoreum and/or anal gland secretions (Rosell & Czech, 2000). Their nocturnal lifestyle allows them to be active at night, engaging in activities like repairing dams, foraging for food, and maintaining their lodges (Gaywood, 2018). During winter, they face challenges due to frozen water bodies and adeptly store food underwater near their lodges to sustain themselves when access to food is limited (Lancia et al., 1982). In addition, subadult beavers display dispersal behaviour in the late winter and early spring (Bloomquist et al., 2012).

Home range is used to describe the spatial use and behaviour of animals (Korbelová et al., 2016a). Burt (1943) defined the home range as: “that area traversed by the individual in its normal activity of food gathering, mating and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered part of the home range.”

Therefore the forming of home ranges is determined by the spatial activity of animals, which tends to concentrate where abundant food resources are available (Horníček et al., 2021; Mitchell et al., 2012). The sizes of home ranges for beavers exhibit seasonal variations, with the shortest ranges occurring in winter, followed by longer ranges in autumn, and the longest ranges observed in spring (Korbelová et al., 2016a). Additionally, the spatial activity of beavers is influenced by habitat type; research suggests that beavers inhabiting river environments tend to have larger home ranges compared to those living within beaver dam systems (Korbelová et al., 2016a). Furthermore, a study conducted by Barták et al. (2013) reveals that at larger spatial scales, the expansion of beaver populations occurs primarily through the gradual occupation of available spaces, known as progressive space-filling, rather than a significant rise in population density. This means that as beaver populations spread out over a given area, they steadily occupy and utilize new suitable habitats instead of concentrating heavily on a few specific regions (Barták et al., 2013).

2.3 The return of the wolf in the Czech Republic

Wolves (*Canis lupus* LINNAEUS, 1758) were once widespread across Europe, Asia and North America up until the Middle Ages (Scherzinger, 2005), but their populations declined significantly over the centuries as a result of habitat loss, hunting, and persecution, especially in the west and central Europe (Hovardas, 2018). However small populations survived in Spain, Portugal, France and Italy (Mattioli et al., 1995; Scherzinger, 2005). The exact timing of when wolves disappeared from various parts of Europe varies, as their decline was a gradual process that occurred over many centuries. By the 1930s, the wolf populations faced extinction in numerous areas within the Western Carpathian range, including the Czech Republic (Bufka & Červený, 2021). Over the past few decades these populations have been recovering, mainly due to improved legislative protection and a reduction in extensive livestock farming practices (Chapron et al., 2014). Hence, from about 2014, the Czech Republic has experienced a swift increase in the spread and growth of wolf populations (Lososová et al., 2021).

2.3.1 Distribution and habitat

One of the most widespread mammals in the world in the past, the wolf's habitat has now been reduced to North America and Eurasia, especially northern Eurasia (Scherzinger, 2005). In Europe, wolf populations are found in parts of Scandinavia, Finland, the Baltic countries, Russia, Belarus, Eastern Poland, the Carpathians, and partially in the Balkans (Scherzinger, 2005). But also in southern and western Europe, from Italy to France and Switzerland, and the Iberian Peninsula (Jędrzejewski et al., 2005).

In recent years, wolves have been distributed across various regions within the Czech Republic. Their presence has notably expanded, although their populations might be more concentrated in certain areas, primarily in the less populated and remote regions of the country. Wolves are now found in various regions including the Orlické Mountains, the Upper Palatine Forest, Moravia, Silesia, and areas connected to the northern territories, such as western Poland, Germany, the Slovak Carpathians, and the Polish Carpathians (Selmy.cz et al., 2022) (Figure 3).

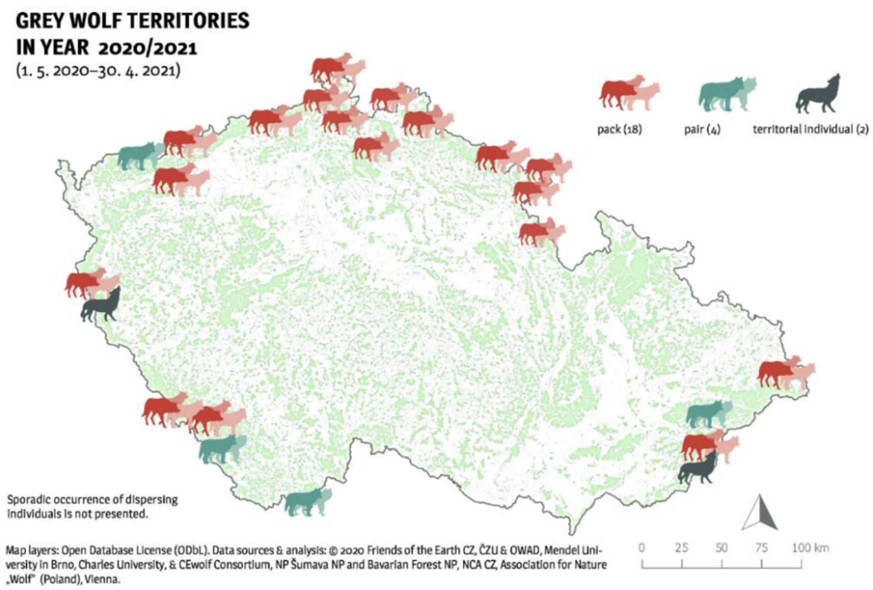

Figure 3 Grey wolf territories in 2020/2021 (Selmy.cz et al., 2022)

Wolves are adaptable animals known to inhabit diverse environments all around the world, but according to Massolo & Meriggi (1998), three important factors exist in determining wolf habitat suitability: wild prey abundance, human absence and forest cover. Wolves often prefer habitats that offer a mix of dense forests, open woodlands (Jędrzejewski et al., 2005), grasslands (Vorel et al., 2023), and remote areas with access to water sources (Kusak et al., 2005; van den Bosch et al., 2023). They tend to thrive in regions where their primary prey, such as deer (*Cervidae* GOLDFUSS, 1820), elk (*Cervus canadensis* ERXLEBEN, 1777), or moose (*Alces alces* LINNAEUS, 1758), is abundant (Massolo & Meriggi, 1998). Additionally, wolves tend to favour areas with minimal human disturbance, as they are typically shy and tend to avoid direct contact with humans (Massolo & Meriggi, 1998). However, in recent times, wolves have shown adaptability by living in some human-altered landscapes, as long as there are suitable prey and less human disturbance (Oakleaf et al., 2006).

2.3.2 Food preferences

Wolves are carnivorous predators with a diverse diet primarily composed of meat, and their food habits can vary depending on the availability of prey in their habitat (Mattioli et al., 2011). Wolves often target large ungulates such as deer, elk, moose, and caribou (Newsome et al., 2016). They are skilled hunters, using teamwork and strategy to take down these animals, particularly focusing on weaker or older individuals within a herd. In addition to larger prey, wolves also hunt smaller mammals like rabbits, rodents, and beavers when larger prey is scarce (Mattioli et al., 1995). In certain areas where wolves and livestock coexist, there have been instances of wolves preying on domestic animals such as sheep, goats, and cattle (Hovardas, 2018). Wolves are opportunistic feeders and may scavenge on carrions or the remains of animals killed by other predators (Newsome et al., 2016). Not least, the wolf has a dietary plasticity that allows it, in the most extreme cases, to feed even on garbage from unregulated dumps (Mattioli et al., 1995). It's important to note that the diet of wolves can be influenced by seasonal variations, prey availability, and human activities in their habitats (Vos, 2000).

2.3.3 Behaviour and spatial patterns

Wolves exhibit a complex social structure that revolves around cohesive pack dynamics, usually comprising a mated breeding pair, their offspring, and occasionally other related individuals (Zimmermann, 2014). Within these packs, communication plays a pivotal role, conveyed through an array of means such as body language, a wide range of vocalizations including distinctive howls (Schenkel, 1967), and the marking of territories with scents (Zimmermann, 2014). Their success as apex predators is attributed to their social structure and hunting tactics, as they are pack animals that cooperate in coordinated hunts to bring down larger prey, owing to their strong jaws and teeth that are adapted for tearing flesh and crushing bones, enabling them to consume most parts of their prey (Mech et al., 2015). These creatures possess a strong sense of territory, which they may assert through vocal displays or, at times, physical confrontations with rival wolf packs (Packard, 2003). Additionally, their behavioural repertoire includes nurturing their young through communal care and cooperation, while pack unity is fundamental for hunting success and overall survival in their ecosystem (MacNulty et al., 2012).

Wolves, being highly adaptable animals, may have shifting spatial patterns and adjust their home ranges in response to changes in prey availability, competition with other wolf packs, and human activities impacting their habitats (Findo & Chovancová, 2004; Kusak et al., 2005).

The spatial patterns of wolves are influenced by various factors such as pack territories, hunting grounds, den locations, and the distribution of resources like prey species and water sources (Findo & Chovancová, 2004; Kusak et al., 2005). Additionally, these animals may travel over long distances in search of prey, leading to dynamic spatial patterns influenced by their hunting strategies and social structures (Findo & Chovancová, 2004; Packard, 2003). However, in areas heavily populated by humans, wolves exhibit reduced movement as they tend to consume human-related food sources like waste dumps and livestock, which are easier prey compared to wild animals (Kusak et al., 2005). Usually, the colonisation of new areas by wolves is a consequence of population increase and dispersal movements, involving especially juveniles and young non-reproductive adults, whose movements are known to be mainly affected by competition for important and scarce resources (Massolo & Meriggi, 1998).

The size of a wolf pack's home range can be extensive, covering hundreds of square miles, especially in areas with scarce prey resources (Jędrzejewski et al., 2007; Vorel et al., 2023). Within this home range, wolves establish dens for raising pups and have specific areas for hunting and resting (Kusak et al., 2005). Their home range size is influenced by several factors including pack size, prey density, and wolf population density, depending also on the level of human activity and the social status of individual wolves in a pack (Findo & Chovancová, 2004). For instance, breeding individuals typically show a regular seasonal pattern, with smaller apparent home ranges observed during the reproduction phase, while nonbreeders do not exhibit any specific patterns in their home range sizes (Vorel et al., 2023). Furthermore, human infrastructure such as roads, trails, and other developments can collectively impact the spatial patterns and home ranges of wolves (Whittington et al., 2005). This impact occurs through habitat fragmentation, degradation, and loss, which can disrupt the contiguous nature of their territories, while vehicle-caused mortality directly impacts their distribution and movement within habitats (Whittington et al., 2005)

2.4 Circadian rhythms

Time is one of the fundamental dimensions in the life of organisms. The daily alternation between light and darkness serves as the primary regulator for rhythmic variations in the behaviour and/or physiology of the majority of species (Vitaterna et al., 2001). Aligned with the sun's descent and ascent, animals engage in sleep and rest, plants undergo the opening and closing of their blossoms, and plankton move upwards and downwards within the water column (Roenneberg & Merrow, 2005).

Circadian (from ‘circa’—about; ‘dies’—a day) rhythms encompass a series of physiological, mental, and behavioural alterations occurring within a 24-hour cycle (Sharma, 2003). These inherent rhythms are primarily regulated by exposure to light and darkness, but also temperature, influencing a broad spectrum of organisms, spanning from animals (humans included) and plants to microorganisms (Beale et al., 2016).

According to Till Roenneberg (2012, p.25), professor of chronobiology, "When living beings are exposed to an environment subject to regular changes, it becomes convenient for them to adapt to these temporal structures, not only to manage changes but also to anticipate them."

2.4.1 Definition

Circadian rhythms are defined operationally as biorhythms based on three key properties (Edery, 2000):

- **Persistence in the Absence of External Cues:** These rhythms continue to function for a period longer than 24 hours even in the absence of external time cues, demonstrating their endogenous nature.
- **Resetting by Environmental Changes:** They are responsive to alterations in environmental conditions, especially the daily cycles of light-dark transitions and temperature changes, which serve as significant cues for their synchronization.
- **Consistency in Period Length Across Temperatures:** Circadian rhythms maintain a consistent period length despite variations in physiologically relevant temperatures, indicating their stability across a wide range of environmental conditions.

An autonomous free-running oscillator might empower animals to stay synchronized to this clock even when they seek shelter in locations with limited or no exposure to light due to adverse weather conditions or unfavourable settings (Edery, 2000).

Extensive experimental evidence supports the idea that the continuation and preservation of a free-running circadian rhythm are attributed to highly specialized internal mechanisms capable of self-regeneration within 24 hours (Gaudi et al., 2000). These mechanisms are commonly referred to as circadian biological clocks. Put simply, circadian clocks are fundamentally made up of a collection of proteins. These proteins, based on specific design principles, create a self-sustaining loop involving transcription and translation processes. This loop operates independently and typically lasts around 24 hours, constituting the core mechanism of these clocks (Edery, 2000). Even in the absence of environmental time cues, these internal clocks retain a period (τ) that approximates 24 hours, exhibiting stability within a physiologically sustainable temperature range (Pittendrigh, 1960).

2.4.2 Circadian rhythms in animals

Unlike humans, animals exhibit a greater number of behaviours that are directly influenced by the light-dark rhythm, such as the timing of hunting, mating for births, and migratory movements (Roenneberg, 2012).

In addition to the three properties mentioned above, there are two other important factors to consider when talking about animals. Circadian rhythms and behaviour of certain species can be influenced by the changing seasons and the phases of the moon (Sánchez-Ferrer et al., 2016), but also by the presence of human activity and predators in the area (Eggermann et al., 2009).

Seasonal changes significantly impact organisms, primarily driven by variations in the amount of light reaching the Earth's surface, influenced by the Earth's axis of rotation. This fluctuation affects the availability of food across different times and regions, leading to reproductive strategies aimed at selecting the optimal mating time. This timing ensures that offspring are born during seasons most conducive to their survival, aligning with periods when food is most abundant (Curi & Taddio, 2013).

The visible effects of the Moon's revolutionary motion around the Earth primarily include the cyclical alterations in the Moon's phases and the fluctuations in tides. Given that approximately 70% of the Earth's surface is covered by oceans, the fluctuating water levels and the nocturnal brightness of the Moon significantly impact these unique ecological habitats, intertwining with the patterns of the circadian cycle (Curi & Taddio, 2013). Animals inhabiting these areas adapt their physiology to synchronize with tidal rhythms (aligned with the tides), semi-lunar rhythms (occurring over 14-day periods), and lunar rhythms (Curi & Taddio, 2013).

Through extensive research and experimentation, it has become evident that circadian rhythms, and occasionally the mechanisms governing these rhythms, display substantial diversity among species belonging to the same classification (Gwinner, 1996). Bio-time management may therefore have adapted to the peculiar dynamics of the individual species. Here I examine the case of the beaver and the wolf.

2.4.3 Beaver

Beavers are primarily active during crepuscular or nocturnal hours, occasionally showing activity in daylight. Their activity period typically ranges from around 17:00 to 08:00 hours (Figure 4), while during the daylight hours, beavers tend to retreat to their lodge or burrow, where they spend their time resting, grooming, and engaging in other activities that help conserve energy and stay protected from potential predators (Swinnen et al., 2015). This behavioural pattern may serve as a strategy to minimize encounters with predators and humans while carrying out their foraging and other essential activities (Mori et al., 2022). On average, the duration of beaver activity throughout the year spans approximately 8 h 12 min ± 1 h 20 min (Mori et al., 2022).

These animals adhere to a relatively predictable circadian rhythm, displaying two distinct activity patterns influenced largely by seasonal changes. During summer, beavers follow a roughly 24-hour circadian rhythm, initiating activities in the mid-afternoon and ceasing in the early morning (Potvin & Bovet, 1975). However, during winter, particularly in regions where ponds freeze, their activity rhythm extends to about 27 hours (Bovet & Oertli, 1974). During such times, beavers often stay in their lodges or under the ice, relying on stored fat reserves and feeding on their cached food supplies (Bovet & Oertli, 1974). Inside their lodge or underwater, consistent low light levels throughout the day make it challenging for beavers to differentiate between sunrise and sunset. Consequently, their activity patterns become less synchronized with the typical solar day, resulting in longer "beaver days" (Bovet & Oertli, 1974).

On the other hand, in regions where temperatures don't cause pond surfaces to freeze, beavers adjust their activity rhythms based on night length (photoperiod) and environmental temperatures. In these conditions, their activity patterns between colder and warmer months typically do not significantly overlap (Mori et al., 2022).

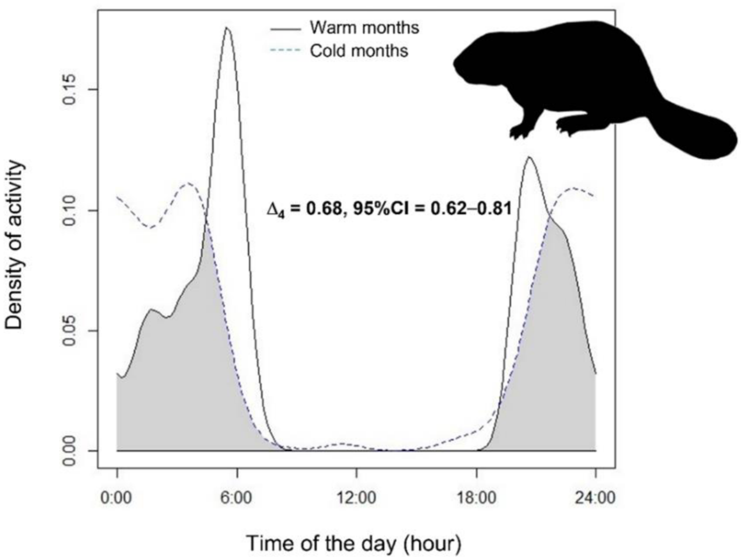

Figure 4: Interseasonal overlap of activity patterns expressed as kernel density estimates (coefficient Δ_4) of the Eurasian beaver in Central Italy; 95%CI = 95% Confidence Intervals. (Mori et al., 2022).

Additionally, studies conducted by Mori et al. (2022) and Swinnen et al. (2015) indicate that beaver activity is influenced by the phases of the moon. Beavers tend to be more active during the darkest nights, decreasing their activity during bright moonlit nights when predators are typically more active (Mori et al., 2022). However, in regions where natural predators are absent, beavers become more active on bright moonlit nights (Swinnen et al., 2015). This shift is attributed to an improvement in foraging success, as their vision is not well-adapted to movements in the dark (Mori et al., 2022).

Another interesting factor exposed by Swinnen et al. (2015) is the influence of the ghosts of predators past. He suggested that the reason why beavers remain active during dawn and dusk, as well as night, isn't solely due to current threats from predators. Instead, the research proposes that their activity patterns reflect a lasting influence from historical predator pressures—a kind of "echo" of past encounters with humans and other predators (Byers, 1998). Beavers have been hunted by humans since ancient times, dating back to the Pleistocene era, and more recent human activities nearly led to the extinction of Eurasian beavers (Mikulka et al., 2022a).

2.4.4 Wolf

The wolf is known to be active mainly at night. However, this does not exclude the fact that wolves may also be active during daylight hours. Some patterns of diurnal activity are known in wolves in wildlife, primarily influenced by seasonal changes, social factors within their pack, and the availability of food resources (Sánchez-Ferrer et al., 2016), but also by human activity and breeding status (Eggermann et al., 2009). On average, they spend around 8 to 10 hours daily in motion, with much of this activity occurring during twilight hours (Eggermann et al., 2009).

Usually, the circadian clock of the wolf is structured as follows: the nocturnal activity begins in the evening, in a span ranging from 17:00–22:00 h, continues through the night and ceases in the morning in a range between 05:00–09:00 h (Ciucci et al., 1997).

Is also interesting to notice how the phases of the moon can influence the circadian clock of wolves. A study conducted by Sánchez-Ferrer et al. (2016) proves that during the crescent moon, wolves show the highest mean of activity while during a full moon phase, the mean activity is significantly decreasing, with the lowest mean activity observed during a new moon.

3. Aim of the study

The primary objective of this thesis is to assess the temporal mechanisms of interspecific coexistence in the Czech Republic, where the Eurasian beaver reappeared after centuries of local absence. In particular, the interest is in the spatiotemporal relationships between the beaver and coexisting predators such as wolves, which returned to the park in 2015.

This study aims to investigate how the reoccurrence of wolves in the Šumava National Park, Czech Republic, has potentially induced changes in the circadian rhythms of beavers. More specifically it aims to describe the circadian activity patterns of beavers in response to the increased presence of wolf populations by integrating data from past studies on territoriality with current field research.

By comparing data on wolf presence with my recent observations (2022-2024) and information gathered by the National Park (NP) administration from 2010-2012, when wolves were not present, I studied how the presence of wolves might have influenced beaver behaviour over an extended period.

The fundamental question addressed is whether beavers are adapting their activity patterns in response to the frequent and regular patrols of wolves. I hypothesize (i) that the presence of wolves influences beaver circadian rhythm, and (ii) that the recent population of beavers are expected to exhibit altered behavioural patterns compared to those observed a decade ago due to the resurgence of wolves, aiming to minimise encounters with the predators (T. D. Gable et al., 2023; Mori et al., 2022).

4. Methodology

4.1 Study area: Sumava National Park

The Šumava National Park (ŠNP) stands as a pristine and enchanting landscape. Situated in the southwestern part of the Czech Republic on the borders with Germany and Austria, the NP is located between three different regions - Český Krumlov, Prachatice, and Klatovy (Figure 5). The park is an ecologically diverse protected region that covers an area of 68,460 hectares (*New Zoning and Tranquillity Areas*, n.d.). Established in 1991, the ŠNP is incorporated as an integral part of the larger Bohemian Forest (Šumava in Czech), which extends across the border into Germany and Austria, making it one of the largest forested areas in Central Europe (*Šumava National Park*, s.d.). The whole territory of ŠNP is a Natura 2000 protected area (Zýval et al., 2016). In 1990 the Šumava NP was included in the list of World Biosphere Reserves, with its peat bogs being an important Ramsar site (Křenová & Hruška, 2012). This park is among the best-preserved natural areas in the Czech Republic (Jačková & Romportl, 2008) and together with the Bavarian Forest NP on the German side, create the largest strictly protected area in Central Europe (Čížková et al., 2011).

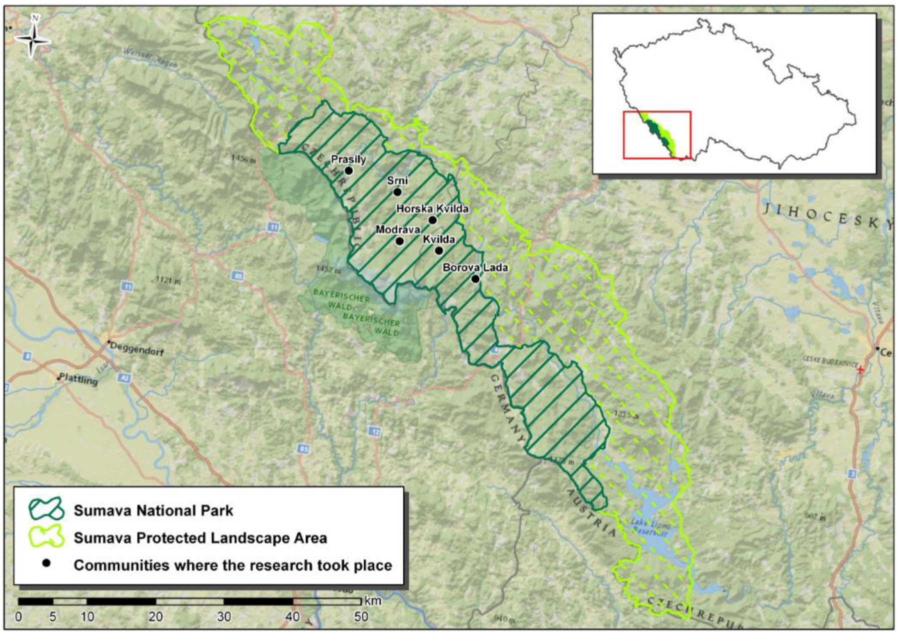

Figure 5: Location map of the Šumava National Park "NP Šumava" and Landscape Protected Area "CHKO Šumava" (Gorner et al., 2012)

The Šumava National Park is mostly covered by woodland, encompassing approximately 80% of its total area, with non-forest regions like pastures, mires, and mountain meadows comprising about 19%, along with a small water area accounting for roughly 1% of the park's territory (Janík, 2020). The park's landscape is characterized by extensive forest ecosystems interwoven with diverse relic habitats, alongside significant semi-natural grassland formations, all enriched by traces of historical human activities (Gorner et al., 2012).

Elevation has an impact on the climate in Šumava, which varies from warm and humid in lower regions to chilly and precipitation-rich in highland plateaux (Jačková & Romportl, 2008). The park is characterized by an average annual temperature ranging from 3.5 to 6.5 degrees Celsius, and an average annual precipitation ranging from 800 to 1600 mm/year (Gorner et al., 2012).

4.1.1 Tree species

Due to Šumava's unique geographical location, the park is home to several endemic plant species, found only within this region (Křenová & Hruška, 2012), which have adapted to the local conditions and play a crucial role in maintaining the ecological balance of the park.

The species composition of forest ecosystems in Šumava National Park exhibits significant variations according to altitude. The prevalent form of vegetation consists of coniferous forests, which have predominantly replaced the original climax deciduous forest stands. Currently, the forest landscape resembles a vast mosaic, encompassing significantly altered, non-native coniferous forest communities as well as nearly untouched, pristine virgin growth areas (Gorner et al., 2012). Šumava National Park is predominantly populated by Norway spruce (*Picea abies*), European beech (*Fagus sylvatica*), silver fir (*Abies alba*), and larch (*Larix*) (Krzystek et al., 2020). A wide range of other tree species can also be found in the park, such as white birch (*Betula pendula*), sycamore maple (*Acer pseudoplatanus*), and common rowan (*Sorbus aucuparia*) (Krzystek et al., 2020).

However, it's important to note that substantial portions of these spruce forests faced severe challenges at the end of the 20th and beginning of the 21st century, primarily due to bark beetle infestations (Stych et al., 2019). Additionally, the landscape underwent further transformations after the storm Kyrill struck in 2007, which caused thousands of trees to be uprooted in mountainous spruce forests. (Zýval et al., 2016). As a result, today's scenery is characterized by the presence of dead spruce trees and young, regenerating forests.

The riparian forest, found along water bodies like rivers and lakes, is a crucial component of the park's ecosystem, stabilizing riverbanks, regulating water quality, and providing habitat for diverse plant and animal species (Chytrý, 2012; Padrtová, 2019). Additionally, it supports a rich mosaic of plant life adapted to riparian conditions, fostering biodiversity and serving as wildlife corridors between different habitats within the park (Fesenmyer et al., 2018). The riparian forests in Šumava National Park, characterized by a rich diversity of tree species like willows, alders, poplars, and birches, provide an essential habitat for many mammals (Krzystek et al., 2020), among which is the beaver. Beavers rely on riparian habitats for food and shelter, primarily feeding on the bark, twigs, and leaves of woody vegetation abundant in these forests (Vorel et al., 2015). Their dam-building activities reshape the environment, expanding riparian forests and creating diverse habitats that support numerous species, fostering ecosystem resilience (Rehaume, 2023). Beaver-modified riparian forests offer ecological benefits such as improved water quality, enhanced habitat diversity, and increased floodplain connectivity (Fesenmyer et al., 2018), underscoring their critical role in Šumava's ecological dynamics.

The vertical stratification of forests, characterized by distinct vegetation layers based on height, influences habitat structure and resource availability for various species (Oliveira & Scheffers, 2018), including beavers. Each layer, from the canopy to the forest floor, supports unique ecological communities, shaping the availability of food resources (Svoboda et al., 2010). Beavers, for example, primarily feed on woody vegetation found in the understory and shrub layers, such as aspen, willow, and poplar, which they use for consumption and in building dams and lodges (Peinetti et al., 2009).

4.1.2 Water stream

The Šumava NP is renowned for its extensive network of water streams, which are integral to its diverse ecosystem that supports a wide variety of plants and animals. These streams flow through dense forests and rugged terrain, playing a critical role in maintaining the park's unique environment (Jačková & Romportl, 2008). Moreover, Šumava forms the primary European watershed between the North and Black Seas, characterized by its naturally high level of water accumulation, including spring areas, peat bog sources, and groundwater (Bucur, 2016).

The park's main rivers, including the Vltava and Otava, are fundamental components of its hydrological system. The Vltava River finds its origins within the boundaries of ŠNP (Křenová & Hruška, 2012). Alongside the Vltava, the Otava River forms another prominent watercourse, together with other major rivers such as the Vydra and Křemelná (Figure 6), which combine to form the river Otava, followed by Volyňka and Blanice (Jačková & Romportl, 2008).

In addition to its rivers, Šumava boasts a variety of lakes, each with its own unique characteristics. Glacial, peat, and anthropogenic lakes dot the landscape, adding to the park's allure and ecological diversity. Notably, the presence of natural glacial lakes, nestled at altitudes of around 1000 meters above sea level, is a remarkable phenomenon (npsumava.cz, s.d.). Lakes such as Laka, Prášilské, and Plešné provide tranquil havens amidst the rugged terrain, serving as vital habitats for aquatic species (*Glacial lakes in the Šumava national park*, 2019).

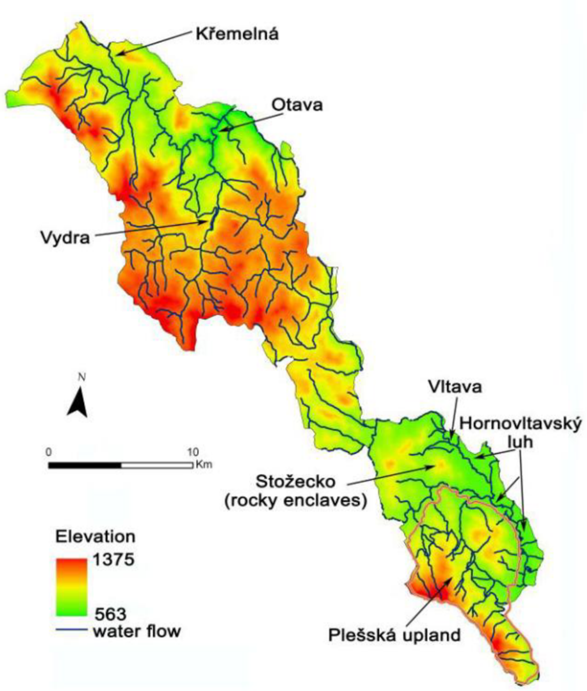

Figure 6: water streams of Sumava National Park (COSMC 2006; Jačková & Romportl, 2008)

4.1.3 The status of beaver populations

As of 2016, the beaver population within Šumava territory was established in 36 locations, with an additional 10 territories outside the park's boundaries indicating a widespread distribution of these industrious rodents (Uhlíková, 2016). Long-term research indicates that the average number of beaver families in the region is between 5 and 7 individuals (Uhlíková, 2016), reflecting a stable and sustainable population and showcasing the adaptability of these creatures to varying habitat conditions. However, occasional reports suggest larger populations of 12 to 15 individuals, which are considered isolated cases and may result from specific environmental factors or transient movements of the animals (Uhlíková, 2016).

The status of Eurasian beaver populations in the Šumava region reflects a dynamic interplay of colonization phases and ecological shades. Initiated in two distinct waves, spanning from 1997 to 2012, the recolonization efforts in Šumava saw the establishment of 44 sites, with a notable concentration observed during the second phase (Vorel et al., 2014). While the western part of Šumava has experienced faster population growth compared to the southern region, both areas saw the establishment of territories, with a total of 16 and 6, respectively, by the winter of 2012 (Vorel et al., 2014). Altitude constraints shape the distribution, with settlements predominantly occurring at altitudes of 700-900 meters above sea level, albeit sporadic sightings at higher elevations highlight the adaptability of these resilient creatures (Vorel et al., 2014). The presence of beavers at such altitudes, including a record of up to over 1000 meters, underscores their capacity to traverse mountainous terrain. In fact, there have been documented instances of a few individuals inhabiting the region at altitudes of up to 1175 meters above sea level, marking the highest recorded elevation for beavers in the Czech Republic (Vorel et al., 2014). Additionally, the period from 2002 to 2012 witnessed significant spread of Eurasian beavers throughout the Czech Republic, with strict criteria for identifying settlements ensuring a strong foundation for studying rapid population development (Vorel et al., 2012). The distribution is divided into three main populations: Moravian, northern Bohemian, and western Bohemian. Remarkably, very large populations live along the Morava and Thaya (Czech: Dyje) rivers, with expansion into surrounding landscapes indicating successful restoration efforts (Vorel et al., 2012).

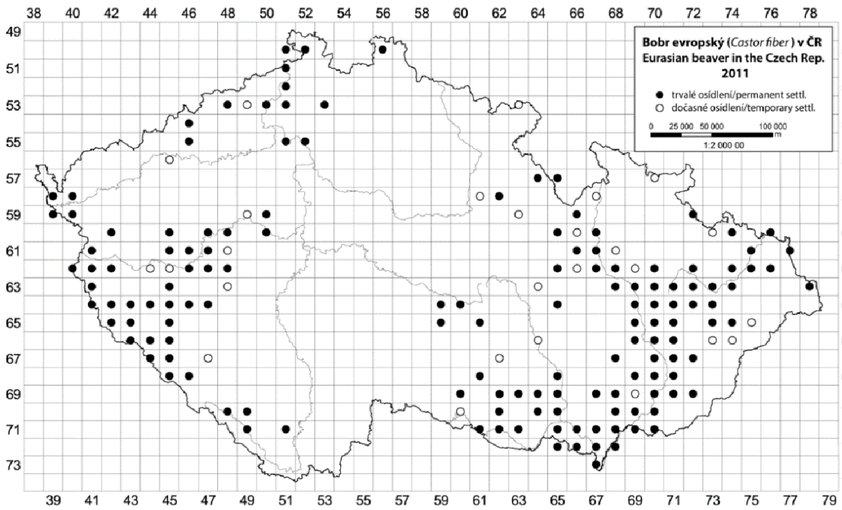

Figure 7: Distribution of the Eurasian beaver (Castor fiber) in the Czech Republic, based on the records summarized at the end of 2011; closed circles – permanent occurrence, open circles – temporary occurrence (Vorel et al., 2012).

4.2 Data collection

When it comes to observing and monitoring beavers, methods can be broadly categorized into two main groups: invasive and non-invasive. The invasive approach involves trapping live beavers, attaching transmitters, and then releasing them. While this method yields the most accurate results, it is time-consuming and carries the risk of accidents that may result in the death of the animal (Vorel et al., 2008). On the other hand, the non-invasive approach, such as the use of camera traps, involves analysing photos after they have been taken. While this method is less invasive, it is also less accurate and depends on the placement of the camera traps (Bijl, 2023).

During this study, it was found that live trapping in conjunction with radio-transmitter deployment proved to be the most effective methodology. The capture of a sufficient sample of beavers and the application of the transmitters were very challenging tasks. It was therefore necessary to work with an experienced team of field surveyors to ensure a sufficient amount of representative sample data. Under the guidance of Aleš Vorel (department of ecology FES CZU, Prague) our team collaborated with several individuals in executing a systematic approach: selecting study sites, trapping beavers, affixing radio-transmitters, and subsequently monitoring them post-release. Alongside another student, I helped in all stages of the project, especially in trapping beavers and afterwards in collecting telemetry data from the beavers during the two years of research. This activity was made feasible through the collaborative efforts of various team members and with the assistance of special permissions granted by the national park authority. Our approach involved several steps: first, selecting the study site; then, trapping live beavers and attaching the radio-transmitters; finally, releasing the individuals and initiating monitoring at least three weeks after release.

Data collection occurred across two distinct seasons, involving different beaver individuals and territories. Primary data collection spanned nearly one year, from October to June 2022/23. During the first season, a total of 7 beavers were monitored, 3 females and 4 males, spanning 5 territories. Secondary data collection occurred during the fall and winter seasons, from October to March 2023/24. In the second part of the project, another 8 beavers were monitored, 1 female and 7 males, covering 6 different territories.

Each beaver was assigned a codename in alphabetical order. The beavers included in this research project for the first season of monitoring were A, B, C, D, E, F, and G. With beavers D and E living in the same family, as well as beavers F and G. During the second season of the project, the beavers monitored were named H, Ch (following the Czech alphabet), I, J, K, L, M and N. With beavers K, L and M living in the same family.

The beaver data monitored in 2008/09 in Český Les and during the period 2010-2012 in the Sumava mountain was provided to me by Aleš Vorel, who personally contributed with his team to the collection of the data.

Furthermore, I utilized information about the wolves provided by the National Park (NP) administration, which regularly monitored wolf populations. The NP administration shared their findings with me, enabling me to assess the potential impact of wolf presence on beaver behaviour and habitat use. The seven wolves were equipped with radio collars, allowing researchers to track their travels over the course of several months.

4.2.1 Site selection

The selection of the trapping sites was based on the presence or absence of beavers and their activity. Another important criterion was transport accessibility, to enable the transport of animals and materials during the trapping. While driving along the park, the presence of beavers was identified through visual observations of fallen trees, ponds, dams, and cuttings. Further confirmation of beaver presence was made on-site by foot trips, focusing on fresh cuttings and recent activity. Territories were deliberately chosen to be as linear as possible, i.e. following the course of the rivers. Additionally, sites were selected based on the presence of wolves; the sites of interest for this research were those where wolf presence was confirmed, indicating cohabitation with beavers.

During the first monitoring season, the selected sites included Horská Kvilda, Březník, Srní, Mechov, and Slunečná. For the second season, the chosen sites were Špičák, Prášily Most, Lanové centrum in Prášily, Železná Ruda, and Modrava (Figure 8).

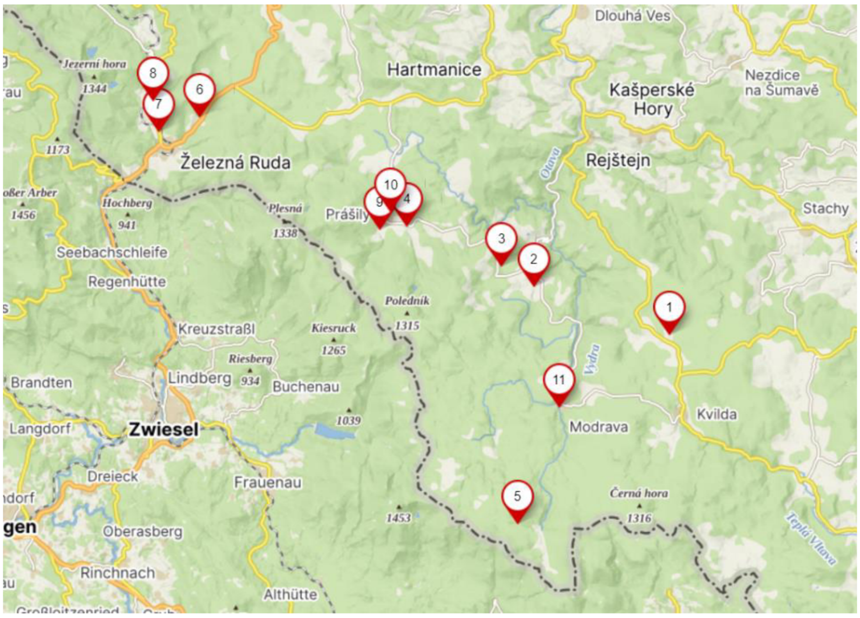

Figure 8: The 11 sites selected in the ŠNP for beaver monitoring: 1) Horská Kvilda 2) Srní 3) Mechov 4) Slunecna 5) Breznik 6) Špičák 7) Železná Ruda 8) Železná Ruda 9) Prášily most 10) Lanové centrum in Prášily 11) Modrava

4.2.2 Trapping and application of transmitter

The traps used were suitcase-style live traps, specifically the Hancock live trap model (Figure 9). These traps feature two spring-loaded jaws surrounded by wire mesh. Positioned in the middle of the trap is a trigger plate that, when activated, causes the trap to close, effectively enclosing the beaver within the wire mesh, like the closing of a suitcase.

Figure 9: a) A Hancock live trap (suitcase-style) set along a streambank with poplar leaves and twigs as bait. b), c) Beaver captured in a suitcase-style live trap using a bank set.

During both seasons, beavers were trapped over an 11-day session in September. Upon identifying a territory with beavers, the best placement to set the trap within the territory was determined. Typically, traps were positioned near the corridors utilized by the beavers to access the water and near their lodge. The traps were always set before dusk. The traps were securely anchored to the bank using a chain and a wooden pole driven deep into the ground, ensuring they remained stable and preventing them from slipping into the water, which could endanger the trapped beaver. Poplar (*Populus*) leaves and twigs, along with a small sample of castoreum, were used as bait to attract the beavers. To ensure safety, warning tape with a sign was installed near each trap to alert onlookers not to approach, thus avoiding any potential incidents (Figure 10). To maximize the likelihood of capture, traps were left at each site for three days, with the bait being replaced daily with fresh bait. Early in the morning, each trap was checked by field patrols and the captured individuals were transferred to a cage for ease of handling, weighing and transporting. Individuals were transported to a makeshift laboratory close to the trapping site, where they were measured, and described in detail. Additionally, blood, faeces, castoreum, and fur samples were collected from each captured beaver for further analysis, an identification chip was implanted in the skin of the neck and a coloured ear tag was fixed in the ear.

Figure 10: warning of danger and presence of a trap.

To monitor the movements of beavers, customised ear tags were used, specifically the M3530 model produced by ATS Inc., which operates at a frequency of 150 MHz. These tags weigh 28 grams and have dimensions of 42 × 52 × 17 mm, equipped with a 200mm antenna (Korbelová et al., 2016b). Each transmitter is assigned a unique frequency number. Following the procedure outlined by Rothmeyer et al. (2002), the antenna was positioned on the tail of the beaver. Before attaching the radio transmitter, the tail area was locally anaesthetized using liquid nitrogen. It was applied by piercing the beavers' tails with the help of a drill and a split cotter pin and shim to secure it (Figure 11). The transmitters were applied only to subadult and adult individuals. Strict hygiene and safety measures were observed to ensure the well-being of both the beavers and the researchers, with special attention given to minimising any discomfort experienced by the beavers during this process. Following the attachment of the transmitter to the tail, the beavers were released at or near the location where they were captured. Over time, the transmitter will naturally detach on its own. Throughout the capture operations, no fatalities or post-operative complications arose due to the transmitter application.

Figure 11: application of a radio-transmitter on the tail with a drill.

4.2.3 Activity record

Telemetry involved the use of a Yagi antenna, receiver, and GPS system to manually collect data (Figure 12). Telemetry activities consisted of an overnight periodic check of tagged individuals. Due to the time and physical demands, a single team, usually consisting of two people, was only able to monitor one, sometimes two, sites at a time. Given that beavers are nocturnal animals, I would set out into the field before sunset and finish after sunrise. In practice, this meant that I spent a minimum of 12 hours per night tracking the animals (from 6 pm to 6 am); in winter, this period extended to 14 hours (from 5 pm to 7 am).

In total, the recording of activity was conducted over a span of five to six nights per month, with each night dedicated to monitoring a different territory. This approach ensured complete coverage for both seasons, as there were five territories to monitor during the first season (2022-2023) and six territories during the second season (2023-2024). The positions of each individual were documented hourly throughout the monitoring period. To prevent spatially correlated data, the shortest interval between two consecutive fixes was consistently set at 30 minutes. In certain cases, practical considerations led to splitting the activity records per territory into two nights. In these cases, the first half of the activity was recorded from 5/6 pm to 12 am, while the second half was recorded from 12:30 am to 6/7 am. One night of telemetry usually produced 20-30 fixes per animal. Data was also collected during the daytime to accurately locate the lodges.

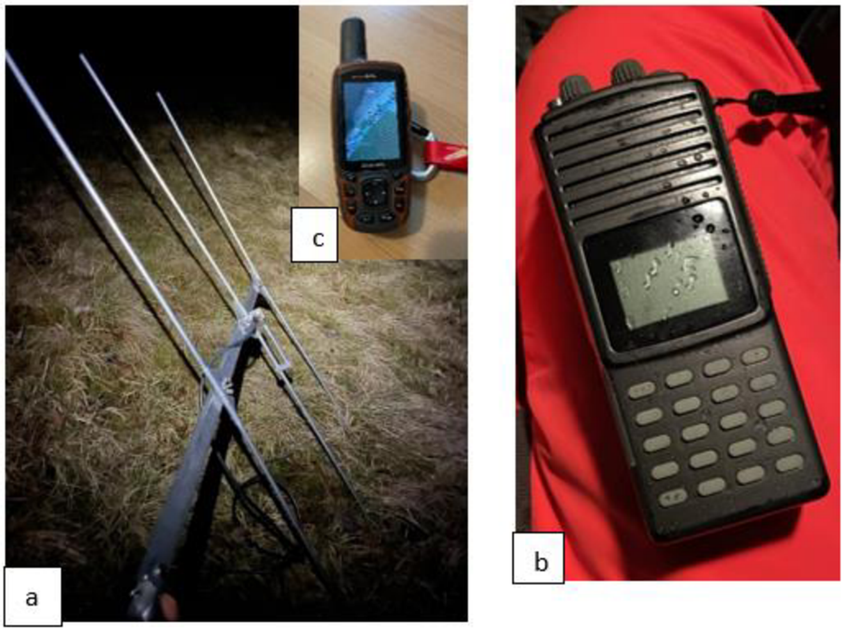

Figure 12: a) antenna, b) receiver and c) GPS Garmin system used for telemetry.

Triangulation, a crucial aspect of telemetry, posed challenges in accurately defining distances between the antenna and the radio-transmitter attached to the beaver. This method relies on measuring the angles between the antenna and the transmitter from different locations to determine the animal's position (Hall, 2020). Fixes were recorded, indicating the strongest signal position with the antenna held perpendicular to the linear water system. However, factors such as dense vegetation, rugged terrain, man-made constructions (such as power poles), and atmospheric conditions can affect the accuracy of triangulation, leading to potential errors in estimating the beaver's location. Additionally, during the tracking period, some individuals had fewer records collected either because they migrated to another territory or were preyed upon by predators. During the first season (2022-2023) a total of two beavers were lost. One male probably dispersed, as he was repeatedly located many km away from the site of capture. Another female also dispersed but no other signs of her have been found. Over the course of the second season (2023-2024) of the monitoring activities, a total of 3 radio transmitters that had fallen off were recovered, plus the carcass of a whole male beaver with the transmitter still attached. It is likely that the discovery of the other three transmitters was also due to a predator killing the beaver. One male probably dispersed, but no other signs of him have been found.

Figure 13: use of triangulation from the roof of a car. Photo by O. Vojtěch

4.3 Data analysis

In total, I analysed three levels of activity: that of wolves, the current activity of beavers, and the historical activity of beavers from 13 years ago.

4.3.1 How will I estimate wolves' presence in beavers' territories

Estimating the presence of wolves within beaver territories was not the primary focus of my thesis; however, I utilized information provided by the National Park (NP) administration, which regularly monitored wolf populations. The NP administration shared their findings with me, enabling me to assess the potential impact of wolf presence on beaver behaviour and habitat use. The methodology for estimating wolf presence involved various techniques, including the collection of field monitoring data such as scat samples, camera trap images, howling observations, and snow tracking. Additionally, wolves were collared, providing valuable data from the collars. Indirect indicators of wolf presence, such as the discovery of animal carcasses and fur, were also considered. The data I will be using originates from GPS tracking of seven individuals between 2021 and 2023, spread out across four wolf territories.

4.3.2 GIS systems

After beaver data were recorded on the GPS, they were transferred to the computer in the form of shapefiles, which were then prepared for upload into the Geographic Information System (GIS). The GIS system utilized for this research is ArcGIS Pro (version 3.2.0, ESRI 2023, Redlands, CA).

4.3.2.1 Transposition of the field data on the streamline

GPS data were acquired either from roads or meadows, necessitating a minimum distance of 50 meters from streams or ponds to prevent disturbance to beaver habitats and potential alteration of data integrity. Consequently, a procedure was devised to transpose the acquired data from terrestrial environments onto riverine habitats to determine precise individual locations along the stream. Initially, the Points Along Line tool was utilized to segment the river line into equidistant points at intervals of 0.5 meters. Subsequently, the Near tool was employed to determine the shortest distance between terrestrial data points and corresponding river points, effectively identifying the nearest point on the river. Input features comprised beaver data points, while output features consisted of river points. The Near tool generated a near table displaying new coordinates, denoted as Near_X and Near_Y, facilitating the transposition of data from XY coordinates to NearXY coordinates, aligning them with river points. This transposition process entailed manual relocation of data points from terrestrial environments to riverine habitats, with snapping enabled to ensure accurate alignment with the river.

Following the successful relocation of beaver points onto the river, the next step involved identifying lodge locations along the riverine habitat for each territory. This task relied on data collected during periods of beaver inactivity, with daytime locations serving as representations for lodge locations. Some beaver families utilized multiple lodges, typically two or three. Upon locating the lodges, buffer zones with a radius of 20 meters were delineated around each lodge to facilitate the visualization of beaver activity patterns. It is necessary to establish a buffer zone due to the potential inaccuracies resulting from measurement errors. This zone serves to mitigate any potential errors in data collection and ensure the integrity of the research results. Points within the buffer zone are likely to indicate behaviours directly associated with the lodge, such as grooming, resting, or caring for offspring, while points outside the buffer zone may represent other activities like foraging or travelling. Therefore locations falling within this defined area were not considered as movement activity, but as staying in the burrow. This division allowed me to count the time that animals spent travelling and the time thy spent near the lodge and not moving.

In handling the old data from 2008/2009 and the period 2010-2012, the same rigorous procedures were applied as with the newly acquired data. Employing the above-mentioned methodology, the old data were transposed onto the riverine habitat. By segmenting the river line into equidistant points and utilizing the Near tool, the old data points were seamlessly aligned with corresponding river points, ensuring consistency in data processing. Furthermore, for this data lodge locations were identified, and buffer zones were delineated.

4.3.3 Analyses on R

In this section, I introduce my analysis conducted in the software program R (version 4.3.3, R Foundation for Statistical Computing, Wien, Austria: www.cran.r-project.org (accessed on 8 March 2024)), comparing recent beaver activity data with historical data from the Šumava National Park previously collected from 2010 to 2012. I utilized the Overlap package (Meredith, Ridout (2024). Overlap: Estimates of Coefficient of Overlapping for Animal Activity Patterns. R package version 0.3.9. URL: https://CRAN.R-project.org/package=overlap) to assess similarities and differences in beaver behaviour activity over time, estimating patterns of interspecific overlap of temporal activity patterns. Analyses were carried out at the annual and seasonal scales (autumn months and winter months). The time of activity is the number of hours the individual was active. This was the time between the moment the animal left the buffer zone and the moment it returned to it and did not leave it again until dawn. Before the analysis, all data representing beavers inside the lodge (data inside the buffer zone) were removed from the dataset, as they were not relevant to the study of the activity.

Seasonal activity was defined using fixes obtained only during the appropriate season; the seasons I set were as follows: autumn (1 October–21 December) and winter (22 December–31 March).

4.3.3.1 Overlap package

The Overlap package in R is an essential tool for evaluating temporal activity patterns observed in camera trap images or GPS recordings, providing information on when animals are most active. This package is specifically built for ecological research and includes functions for computing overlap indices, doing geographical analyses, and creating visualizations to analyse patterns of co-occurrence or activity overlap among species, revealing potential predator-prey dynamics or competitive interactions (Ridout & Linkie, 2009). The package's features allow for the quantification of overlap as well as the estimation of confidence intervals using bootstrap methods (Meredith et al., 2024). The Overlap package is extremely valuable for gaining insights into ecological relationships and dynamics, whether it is examining animal temporal activity patterns, investigating spatial interactions between species, or researching habitat preferences. The time unit is defined as a day, with values ranging from 0 to 1. The overlap package operates exclusively in radians, facilitating the fitting of density curves through the utilization of trigonometric functions (such as sin, cos, and tan), thus expediting bootstraps and simulations (Meredith & Ridout, 2018). Therefore, time values needed to be converted using a simple and direct equation:

```
timeRad <- data$Time * 2 * pi
```

A two-step procedure for quantifying the extent of overlap between two activity patterns, based on a sample from each dataset (Recent data **Rd** and Historical data **Hd**), was performed. In the first step, each activity pattern was estimated separately, employing non-parametric techniques, using kernel density estimation.

For the second step, I estimated the coefficient of overlapping (Δ) between the temporal activity patterns of current beavers with those studied more than a decade ago within the Šumava National Park. The coefficients of overlapping ranged from 0 (no overlap) to 1 (complete overlap) (Meredith & Ridout, 2018). This is defined as the area under the curve that is created by taking the minimum of the two density functions at each time point (Linkie & Ridout, 2011). Ridout & Linkie (2009) discussed three alternative ways of estimating Δ, given estimates of the two probability density functions. These were labelled $\Delta\hat{}_1$, $\Delta\hat{}_4$ and $\Delta\hat{}_5$ for consistency with earlier work. Here, I use their estimators $\Delta\hat{}_1$ and $\Delta\hat{}_4$, which were recommended for ‘small’ (less than 50) and ‘large’ (greater than 75) sample sizes, respectively (Meredith & Ridout, 2018). Then, I estimated the 95% confidence intervals (hereafter, 95% CI) of the coefficient estimator based on 10,000 bootstrap samples. The temporal overlap was considered high if $\Delta > 0.75$, intermediate if $0.50 < \Delta < 0.75$, and low if $\Delta < 0.50$ (Mori et al., 2022). When confidence intervals are close to 0 or 1, it indicates uncertainty about the size of the difference between the measurements being compared. On the contrary, when the confidence intervals are not close to 0 or 1, it suggests that the difference between the measurements is likely important and not just due to random chance. This helps in understanding whether the observed patterns or results are meaningful or simply random fluctuations.

The exact same approach above-mentioned was used at a seasonal scale, for comparison of autumn and winter months between recent beaver data (2022-2024) and historical beaver data (2008/2009 and 2010-2012).

5. Results

5.1 Beaver telemetry

In the course of the research, a total of 15 animals were captured and equipped with a transmitter. In September 2022, 7 beavers, 3 females and 4 males, were radio-tagged in a total of 5 territories (Table 1). Three territories with one individual (one female and two males), and two territories with two individuals (one female and one male in both cases). During the first season of monitoring, the recording of movement activity took place from October 2022 to June 2023, with one animal lost in February and one lost in March. It was not possible to ascertain whether the animals had dispersed in search of another territory or had been killed by a predator. The total number of samples collected consists of 1007 GPS locations.

Table 1: detailed list of individuals monitored during the Season 2022-2023

	Beaver	Territory	Date of capture	Telemetry			Comments
				Start	End	Total no. of fixes	
1	A	Horská Kvilda	15/09/2022	02/10/2022	25/02/2023	137	Went dispersed in March
2	B	Březník	15/09/2022	15/10/2022	08/03/2023	128	Beaver on the territory with the highest altitude (1200 m a.s.l.)
3	C	Srní	17/09/2022	22/10/2022	16/01/2023	125	Lost in February
4	D	Mechov	17/09/2022	30/09/2022	16/06/2023	158	
5	E	Mechov	17/09/2022	30/09/2022	16/06/2023	156	
6	F	Slunečná	17/09/2022	16/10/2022	15/04/2023	136	
7	G	Slunečná	17/09/2022	16/10/2022	15/04/2023	167	
Total						**1007**	

In September 2023, a total of 8 beavers were captured and radio-tagged, 1 female and 7 males spanning six territories (Table 2). Five territories with one individual (all of them males), and one territory with three individuals (one female and two males). During the second campaign of monitoring, the recording of movement activity took place from October 2023 to March 2024. The total number of samples collected consists of 899 GPS locations. One animal went lost in December, three animals in February and one went lost in March. It was not possible to ascertain for all the missing beavers whether the animal had dispersed in search of another territory or had been killed by a predator. However, it is easier to deduce the events surrounding the disappearance of two beavers (K and L). The transmitter of individual K was recovered in the middle of a field near its territory, with a tiny old piece of tail still attached. Moreover, the transmitter was still equipped with a bolt and a shim that were used to secure it to the tail, which suggests that the transmitter did not detach itself. These two factors suggest that the beaver was probably the victim of some predator, most likely the wolf. Another factor to be considered, but which is impossible to be certain of, is that the skull of a beaver (which could not be ascertained, however) was also found in the vicinity of the territory of individual K.

On the other hand, it is more certain what happened to individual L, whose body was found with a lacerated abdomen, with the transmitter still attached (Figure 14). The stomach and intestines were found a few metres from the body. In this case, it is easier to ascertain death by a predator because the wounds did not suggest killing by a human. Instead, the chewed ribs suggest depredation by wolves. In addition, it is assumed that if he had been killed by a human, the human would not have left the transmitter attached to the body.

Figure 14: dead beaver L with chewed ribs and the transmitter still attached to the tail

The disappearance of the individual Ch is a bit more mysterious. The transmitter was found and retrieved in a pasture some meters away from the water, but there was no trace of the beaver, neither fur, blood, nor any other evidence suggesting predation by the wolf.

Table 2: detailed list of individuals monitored during the Season 2023-2024

	Beaver	Territory	Date of capture	Telemetry			Comments
				Start	End	Total no. of fixes	
1	H	Tůmův most	17/09/2023	07/10/2023	17/01/2024	98	Went missing in February
2	Ch	Lanové centrum (Prášily)	18/09/2023	07/10/2023	17/01/2024	93	Found transmitter on February 11, 2024; missing animal
3	I	Špičák	21/09/2023	13/10/2023	17/03/2024	129	
4	J	Železná Ruda	23/09/2023	14/10/2023	17/03/2024	141	
5	K	Špičák (viaduct)	24/09/2023	13/10/2023	28/12/2023	83	Found the transmitter on February 17, 2024; missing animal. Probably beaver went missing in December
6	L	Špičák (viaduct)	24/09/2023	13/10/2023	15/01/2024	113	Found fresh dead body on February 17, 2024. Probably eaten by wolf
7	M	Špičák (viaduct)	24/09/2023	13/10/2023	17/03/2024	124	
8	N	Modrava	16/10/2023	28/10/2023	11/02/2024	118	Went missing in March
Total						899	

The founding of the detached transmitters and the discovery of a deceased beaver will have both positive and negative implications for research. While the inability to further record the activity of four out of eight beavers in 2024 due to missing individuals represents a loss of data, these findings also confirm the presence of wolves in the Šumava NP and their ongoing predation on beavers.

The presence of the wolf in the same territories as the beavers is further confirmed by the radio collar data. By comparing the records of beavers with the one of followed wolves, is visible how the territories match and overlap. In Figure 15, it is evident how the wolf territories overlap with those of the beavers monitored between 2022 and 2024.

Figure 15: In yellow wolves' territories, in red beavers' territories

After processing the beaver data in the GIS program, the visible result for each beaver territory is as follows: a line representing the river, the red dots on the line representing the position of the beaver during its activity (total activity recorded during the telemetry campaign), and the yellow dots representing the lodge with its buffer zone (Figure 16).

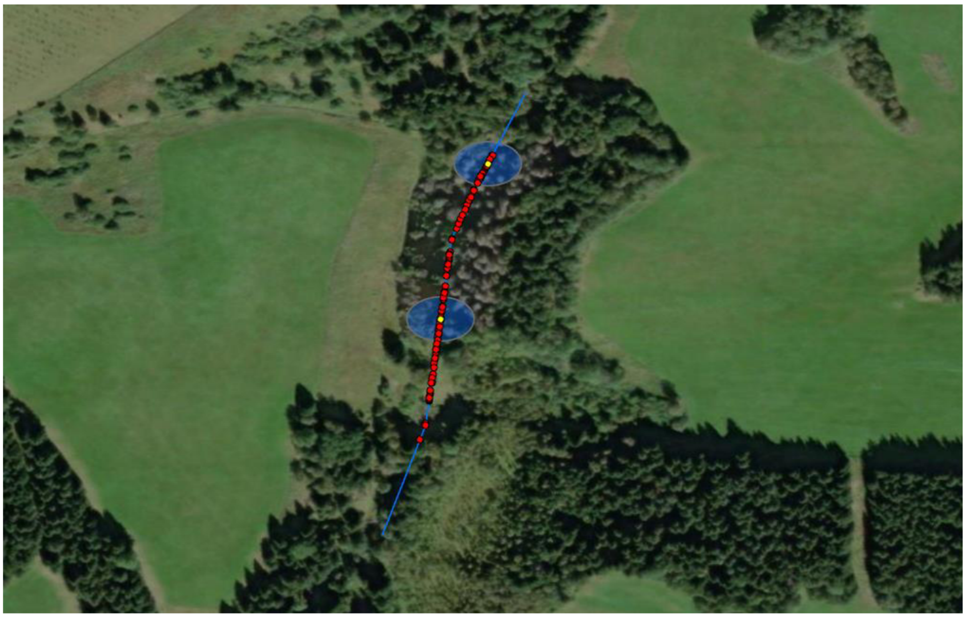

Figure 16: Example of how it looks on GIS. Cyril territory. The red points represent the location collected throughout the telemetry process, indicating where the beaver was located during each night of telemetry; in yellow the lodges; in blue the buffer zone of 20 metres around each lodge

5.2 Length of activity in the absence of wolves

Using the overlap procedure for data analysis, the resulting graphs show an x-axis indicating the time of day, ranging from 00:00 to 24:00, and a y-axis representing the density of beaver activity. Within the graph, there is a representation of the activity pattern observed between the hours of 21:00 and 03:00, serving as a reminder that the density of activity follows a circular pattern.

The data collected from the period 2008-2012 reveals distinct patterns in beaver activity throughout the day (Figure 17). There are two prominent peaks in activity during the nighttime hours, with a primary peak occurring in the early half of the night around 22:30, followed by a decline in activity around midnight, and a secondary peak in the second half of the night around 05:00. Activity starts at approximately 17:00, indicating the onset of beaver activity, and continues until around 08:00, marking the end of activity. Two distinct periods within the 24-hour cycle demonstrate a significant increase in the density of activity of monitored beavers: one around 06:00, coinciding with sunrise, and the other around 18:00, corresponding to sunset.

During the midday hours (12:00 to 18:00) and late-night hours (around 24:00), there is a noticeable decline in the activity density of monitored beavers, suggesting reduced activity levels during these two periods.

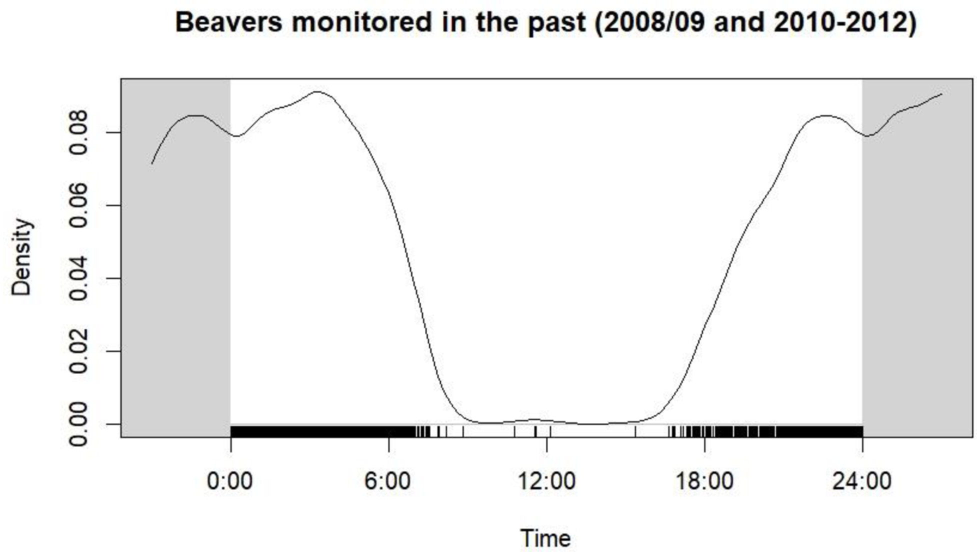

Figure 17: Fitted kernel density curve for beavers monitored in the period 2008-2012, using default smoothing parameters. Daytime data are not to be considered.

Graphical representations of seasonal activity show marked differences between autumn and winter (Figure 18). In autumn, the activity pattern shows two distinct peaks: one occurring during the first half of the night at 22:30 and a larger peak observed in the second half of the night at 04:00, with a decrease in activity around midnight. The activity typically begins around 17:00 and ends at 08:00. In contrast, during the winter months, the activity pattern shows a slight variation, characterised by a single peak of activity, big and well-defined, occurring in the latter part of the night at around 04:30-05:00. The activity typically starts around 17:00 and ends at 08:00.

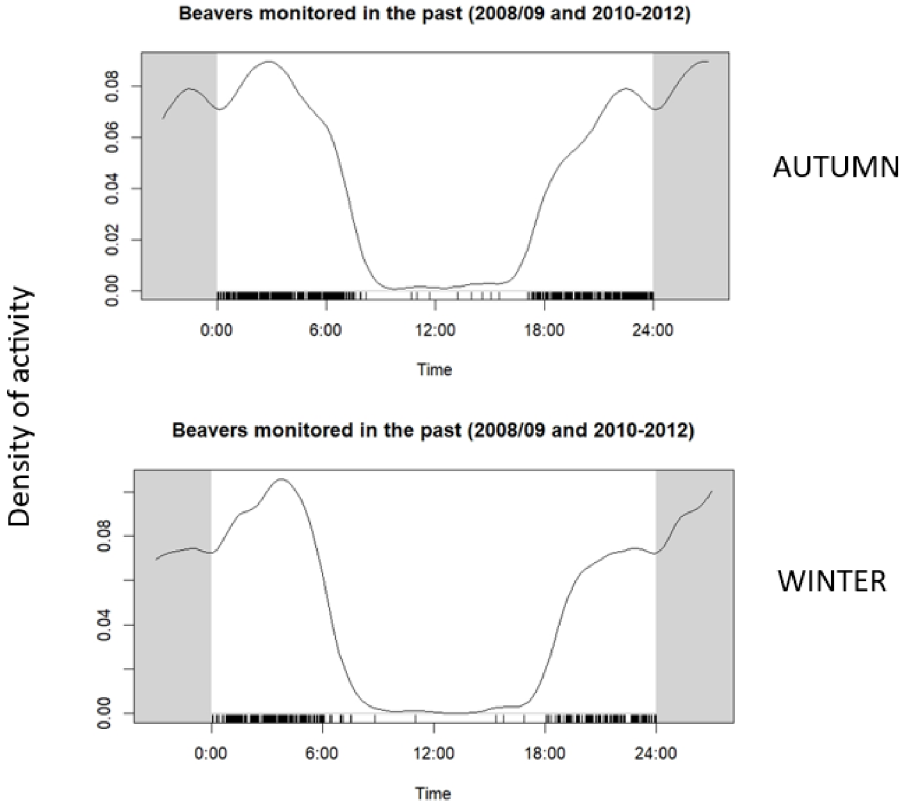

Figure 18: Fitted kernel density curve for beavers monitored in the total period 2008-2012, separated by season (autumn and winter). Daytime data are not to be considered

5.3 Length of activity under wolf presence

The beavers I monitored showed a concentrated activity between 18:00 and 06:00, with one peak at midnight (Figure 19). During the diurnal hours the activity is very low, less than 20%. Activity starts to increase rapidly after 18:00, reaching 60% around 20:00. The maximum peak of activity, almost 100%, occurs around midnight. After midnight, activity gradually declines and drops to daytime lows.

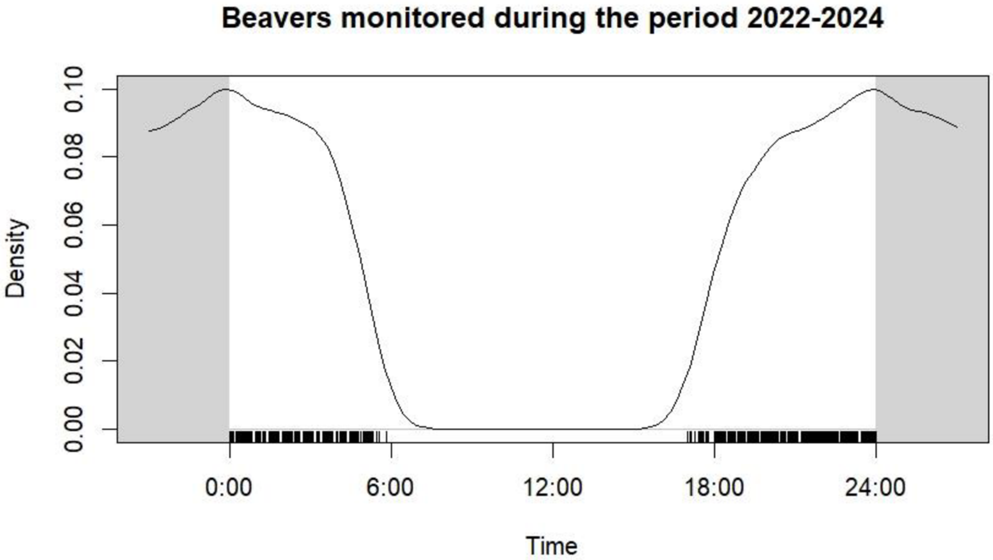

Figure 19: Fitted kernel density curve for beavers monitored in the period 2022-2024.

In autumn (Figure 20), the data indicate two peaks of activity among beavers: one observed shortly before midnight, followed by another peak occurring shortly before the decrease in activity, around 05:00. The start of activity is observed at 16:00 and persists until 06:00. In contrast, in winter, a single, consistent peak of activity is observed at midnight. Activity typically begins around 18:00 and persists until 06:00.

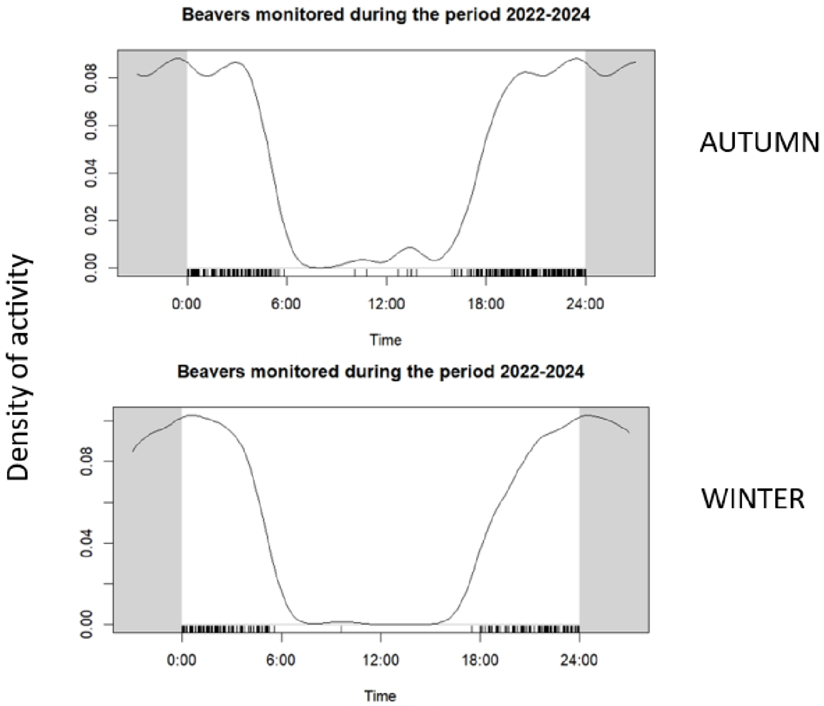

Figure 20: Fitted kernel density curve for beavers monitored in the period 2022-2024, separated by season (autumn and winter). Daytime data are not to be considered.

5.4 Comparison of circadian rhythms

The following graphs (Figure 21), obtained using the R overlap package, show the density of monitored beaver activity in two different periods: the first between 2022 and 2024, represented by the solid line, and the second combining the periods 2008/09 and 2010-2012, represented by the dashed line. The shaded area in the graph indicates the overlap of beaver activity between the two periods monitored. The overlap represents the times of day when beavers show similar behaviour in terms of activity in both the historical and recent periods.

The overlap coefficient (Δ_4) of 0.85 is a quantitative indication of this overlap. A value of 0.85 indicates a high degree of similarity between the two datasets. In other words, beaver activity in the two periods is very similar most of the time. The 95% confidence interval (95% CI) ranging from 0.82 to 0.88 provides an estimate of the uncertainty associated with the overlap coefficient. This interval indicates that if monitoring were repeated many times, the true value of the overlap coefficient would fall between 0.82 and 0.88 in 95% of the cases. The narrowness of this interval suggests that I am confident in the estimate of the overlap.

The overlap is most evident in the early morning hours, starting shortly after midnight until about 06:00, and then again in the evening, starting about 17:00 until midnight. There is a visible difference in the peaks of activity. For recent beavers, there is only one peak during the night at midnight, while for historical beavers the graph shows 2 distinct peaks: one in the first part of the night at around 22:00 and the second peak in the later part of the night at around 05:00.

There is also a difference between seasons. In autumn beavers nowadays activate earlier than beavers in the past, both in autumn and in winter. Also, the end of activity arrives much earlier for beavers of nowadays compared to beavers in the past. The results show a 95% CI ranging between 0.81 and 0.89 for autumn months against the 95% CI of 0.79-0.9 for the winter months. The peaks of activity differ between the seasons. For recent beavers, in autumn the visible peaks are three. One peak at 18:00, one right before midnight, and a third one at around 04.30 in the morning. For historical beaver the peaks represented in the graph are two: one peak at around 22:30 and the other at 04:00. In winter there is one peak for recent beaver at midnight while for historical beaver is visible a very smooth peak just right after activation and another one more big and pronounced at 05:00.

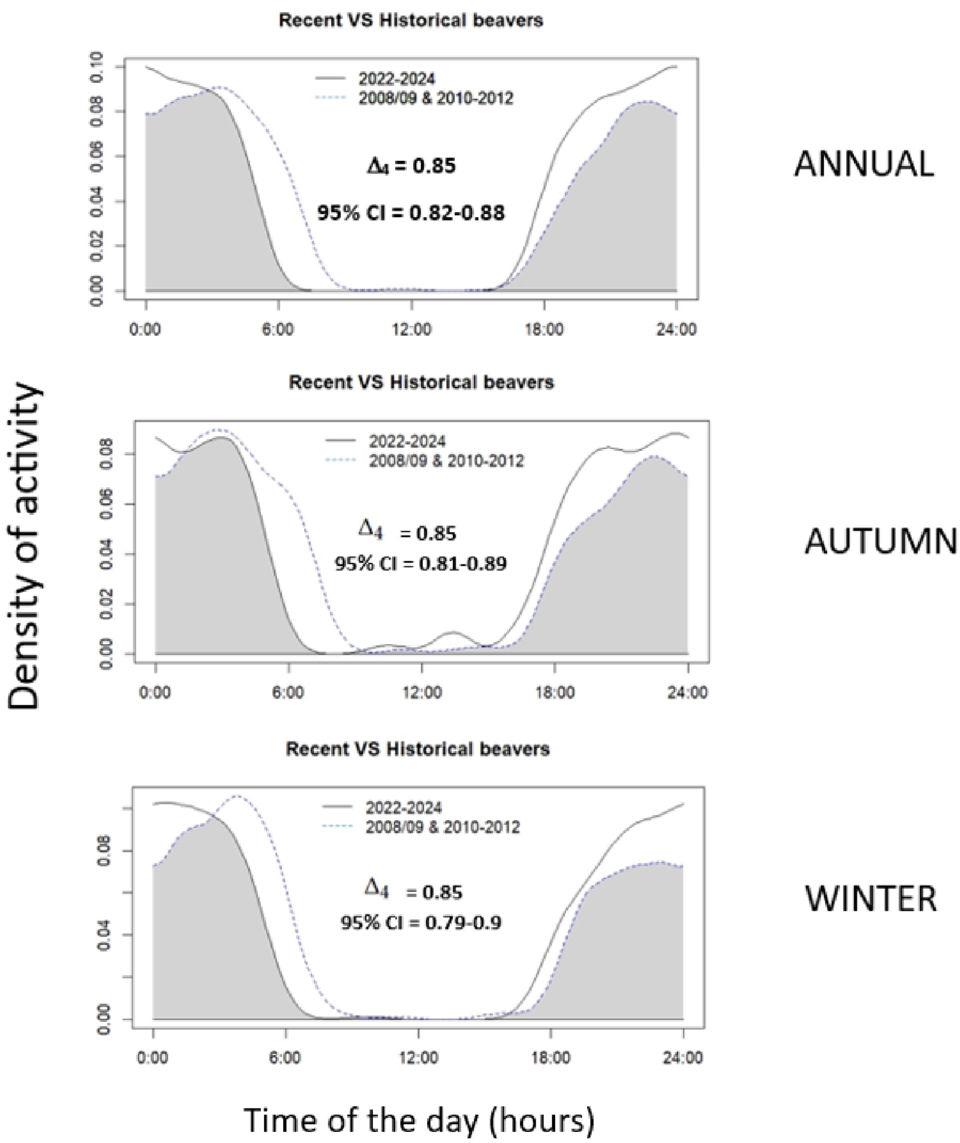

Figure 21: Interspecific overlap of activity patterns expressed as kernel density estimates (coefficient Δ4) between the Eurasian beavers monitored between 2008-2012 and the beavers monitored between 2022-2024.; 95%CI = 95% Confidence Interval

6. Discussion

In this study, I investigated the activity rhythms of Eurasian beavers within the Šumava NP study area. The activity patterns determined during this research were compared with those observed in the same territory, but also in Český les, over a decade ago, when the wolf was absent. The aim of this comparison was to assess whether contemporary beaver behaviour has undergone any alterations in the circadian rhythm, particularly following the reintroduction of wolves to the same areas inhabited by beavers.

Sunset turns out to be the reference point for the start of beaver activity, indicating their preference for crepuscular and nocturnal behaviour. This aligns with previous research confirming the Eurasian beaver's tendency to be active during twilight and night-time hours (Swinnen et al., 2015). Throughout the year, beavers consistently avoid daytime hours, a behavioural strategy also observed in various prey species, likely aimed at reducing encounters with predators and poachers (Mori et al., 2022).

The results of my study indicate a significant overlap in the activity patterns of beavers when comparing circadian rhythms between two periods: one running from 2022 to 2024 and the other combining data from 2008/09 and 2010-2012. In particular, the overlap is most pronounced during the early morning hours and again in the evening, emphasising consistent patterns of activity across periods. In general, contemporary beavers show earlier activation and cessation of activity than their historical counterparts, both annually and in autumn and winter. Approximately recent beaver stops their activity at 6:00 in the morning, while past beavers end their activity at 8:00. This confirms that the current beavers have slightly modified their behaviour compared to those of the past. The peaks in the graphs indicate diurnal variations in beaver behaviour, emphasizing their preference for activity during particular times of the day, especially around sunrise and sunset.

Analysing these results in relation to beavers found dead and presumably killed by wolves, it emerges that the change in the circadian rhythm of today's beavers is partly attributable to the return of wolves to the area. Although the graph shows no significant differences between the two periods, both of my initial hypotheses can be confirmed. The presence of the wolf influences the circadian rhythm of the beavers; and the recent population of beavers in Šumava NP exhibits altered behavioural patterns compared to those observed more than a decade ago, which is due to the reappearance of the wolf in the territory. It can be assumed that the beavers have reduced their activity in the early morning hours to avoid possible encounters with this predator, which is mostly crepuscular (Ciucci et al., 1997). On the other hand, the difference between autumn and winter is not so pronounced. However, some patterns show a slight seasonal variation in beaver activity, reflecting behavioural adaptations probably influenced by environmental changes and seasonal factors (Mori et al., 2022).

Nonetheless, it's essential to acknowledge the limitations encountered during this study. Technical and logistical challenges associated with the use of telemetry contributed to not-so-precise data collection. The accuracy of beaver telemetry is lower than from other types of data collection (e.g. GPS collars), compromising the quality of the data collected and limiting the ability to accurately track beaver movements and activities.

For a more comprehensive investigation, I would like to indicate the use of bio-logging, which allows data to be recorded in the device's memory. In this way data collection is not interrupted by signal loss, and allows users to assemble large, near-continuous datasets of a wide range of data types (Mayer et al., 2022). However, this type of device is very expensive and can only collect data for a duration of two months as the battery drains quickly. Moreover, the animals monitored by this device should be recaptured to retrieve the data. Furthermore, I suggest waiting for the development of advanced beaver monitoring technologies to obtain the most accurate results possible, approaching 100% accuracy. In the near future is not so difficult to imagine the invention of innovative technologies that could include continuous monitoring systems that allow 24-hour tracking of individuals, including movements and activities within dens. By using these advances, researchers could gain a deeper understanding of beaver behaviour and ecology, leading to more informed conservation decisions and management strategies.

Comprehending the dynamics between wolves and beavers is crucial for interpreting ecosystem interactions within Šumava National Park. The presence of wolves can potentially impact beaver behaviour, leading to alterations in activity patterns, habitat selection, and population dynamics. Integrating data on wolf presence with research findings on beaver activity and habitat use facilitates a more comprehensive understanding of ecological dynamics within the park. This interdisciplinary approach provides valuable insights into the complex relationships between predator and prey species and their effects on ecosystem structure and function.

7. Conclusion

In summary, a total of 15 beavers were captured and fitted with a transmitter, with 7 beavers tagged in September 2022 and 8 in September 2023. The monitoring period extended from October 2022 to June 2023 for the first group and from October 2023 to March 2024 for the second group, with a total of 1906 fixes collected between the two periods.

During the monitoring, several beavers went missing, with some presumed to have been killed by predators, as transmitters of two beavers were found detached, one with indications of wolf predation (beaver K) and another with clear evidence of predation by wolves (beaver L). The presence of wolves in the area was thus confirmed by these incidents, indicating ongoing predation on beavers.

GIS analysis revealed the territories of monitored beavers, with data showing their movements along rivers and the locations of their lodges. The overlap of wolf and beaver territories further confirms the coexistence and interactions between the two species.

Analysis of beaver activity patterns showed significant similarities between recent data (2022-2024) and historical data (2008-2012), with a high overlap coefficient of 0.85. Beaver activity was concentrated during nighttime hours, with peaks observed around midnight. Seasonal variations in activity patterns were observed, with differences between autumn and winter, both historically and in recent data.

Comparison of circadian rhythms between recent and historical data showed similarities but also differences in peak activity times. Recent beavers showed earlier activation and cessation of activity compared to historical beavers, especially noticeable in autumn months. Peak activity times varied between recent and historical beavers, with recent beavers exhibiting more peaks, especially in autumn.

In conclusion, this research offers valuable insights into beaver behaviour, predator-prey interactions, and the influence of environmental factors on activity patterns, enriching our comprehension of ecosystem dynamics within the study area. The findings highlight the consistent circadian rhythms of Eurasian beavers, showcasing their adaptability in the face of changing environmental conditions and predator reoccurrence. The earlier activity shifts observed in contemporary beavers suggest adaptive responses to mitigate predation risks, emphasizing the intricate balance between predator-prey dynamics and ecological processes.

8. References

Anderson, C. B., & Rosemond, A. D. (2007). Ecosystem engineering by invasive exotic beavers reduces in-stream diversity and enhances ecosystem function in Cape Horn, Chile. *Oecologia*, *154*(1), 141–153. https://doi.org/10.1007/s00442-007-0757-4

Apfelbach, R., Blanchard, C. D., Blanchard, R. J., Hayes, R. A., & McGregor, I. S. (2005). The effects of predator odors in mammalian prey species: A review of field and laboratory studies. *Neuroscience & Biobehavioral Reviews*, *29*(8), 1123–1144. https://doi.org/10.1016/j.neubiorev.2005.05.005

Baker, B. W., & Hill, E. P. (2003). Beaver (Castor canadensis). In P. D. George A. Feldhamer, P. D. Bruce C. Thompson, & P. D. Joseph A. Chapman (A c. Di), *Wild Mammals of North America* (pp. 288–310). Johns Hopkins University Press. https://doi.org/10.56021/9780801874161

Barták, V., Vorel, A., Šímová, P., & Puš, V. (2013). Spatial spread of Eurasian beavers in river networks: A comparison of range expansion rates. *The Journal of animal ecology*, *82*. https://doi.org/10.1111/1365-2656.12040

Basey, J., & Jenkins, S. (1995). Influences of predation risk and energy maximization on food selection by beavers (Castor canadensis). *Canadian Journal of Zoology*, *73*, 2197–2208.

Beale, A. D., Whitmore, D., & Moran, D. (2016). Life in a dark biosphere: A review of circadian physiology in “arrhythmic” environments. *Journal of Comparative Physiology B*, *186*(8), 947–968. https://doi.org/10.1007/s00360-016-1000-6

Berg, E. van den. (2023, giugno 18). MENDELU Researchers Conduct Research On Beaver Parasites, Population, and Meat Quality. *Brno Daily*. https://brnodaily.com/2023/06/18/science/mendelu-researchers-conduct-research-on-beaver-parasites-population-and-meat-quality/

Bloomquist, C., Nielsen, C., & Shew, J. (2012). Spatial Organization of Unexploited Beavers (Castor canadensis) in Southern Illinois. *The American Midland Naturalist*, *167*, 188–197. https://doi.org/10.1674/0003-0031-167.1.188

Bovet, J., & Oertli, E. F. (1974). Free-running circadian activity rhythms in free-living beaver (Castor canadensis). *Journal of Comparative Physiology*, *92*(1), 1–10. https://doi.org/10.1007/BF00696522

Bucur, D. (2016). *River Basin Management*.

Bufka, L., & Červený, J. (2021). *The grey wolf (Canis lupus) in southwestern Bohemia (Czech Republic): The beginning of new expansion in a long-term perspective*.

Burt, W. H. (1943). Territoriality and Home Range Concepts as Applied to Mammals. *Journal of Mammalogy*, *24*(3), 346–352. https://doi.org/10.2307/1374834

Byers, J. A. (1998). The Ghosts of Predators Past. In *American Pronghorn: Social Adaptations and the Ghosts of Predators Past* (pp. 234–244). University of Chicago Press. https://press.uchicago.edu/ucp/books/book/chicago/A/bo3620573.html

Chapron, G., Kaczensky, P., Linnell, J., von Arx, M., Huber, D., Andrén, H., López-Bao, J. V., Adamec, M., Álvares, F., Anders, O., Balciauskas, L., Balys, V., Bedő, P., Bego, F., Blanco, J., Breitenmoser, U., Brøseth, H., Bufka, L., Bunikyte, R., & Boitani, L. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science*, *346*, 1517–1519. https://doi.org/10.1126/science.1257553

Chytrý, M. (2012). Vegetation of the Czech Republic: Diversity, ecology, history and dynamics. *Preslia*, *84*, 427–504.

Ciechanowski, M., Kubic, W., Rynkiewicz, A., & Zwolicki, A. (2011). Reintroduction of beavers Castor fiber may improve habitat quality for vespertilionid bats foraging in small river valleys. *European Journal of Wildlife Research*, *57*(4), 737–747. https://doi.org/10.1007/s10344-010-0481-y

Ciucci, P., Boitani, L., Francisci, F., & Andreoli, G. (1997). Home range, activity and movements of a wolf pack in central Italy. *Journal of Zoology*, *243*(4), 803–819. https://doi.org/10.1111/j.1469-7998.1997.tb01977.x

Čížková, P., Svoboda, M., & Krenova, Z. (2011). Natural regeneration of acidophilous spruce mountain forests in non-intervention management areas of the Šumava National Park – the first results of the Biomonitoring project. *Silva Gabreta*, *17*, 19–35.

Curi, U., & Taddio, L. (2013). *Pensare il tempo. Tra scienza e filosofia* (Filosofie). Mimesis. https://www.ibs.it/pensare-tempo-tra-scienza-filosofia-libro-vari/e/9788857517865

Edery, I. (2000). Circadian rhythms in a nutshell. *Physiological Genomics*, *3*(2), 59–74. https://doi.org/10.1152/physiolgenomics.2000.3.2.59

Eggermann, J., Gula, R., Pirga, B., Theuerkauf, J., Tsunoda, H., Brzezowska, B., Rouys, S., & Radler, S. (2009). Daily and seasonal variation in wolf activity in the Bieszczady Mountains, SE Poland. *Mammalian Biology - Zeitschrift fur Saugetierkunde*, *74*, 159–163. https://doi.org/10.1016/j.mambio.2008.05.010

Fesenmyer, K. A., Dauwalter, D. C., Evans, C., & Allai, T. (2018). Livestock management, beaver, and climate influences on riparian vegetation in a semi-arid landscape. *PLoS ONE*, *13*(12), e0208928. https://doi.org/10.1371/journal.pone.0208928

Findo, S., & Chovancová, B. (2004). *Home ranges of two wolf packs in the Slovak Carpathians*.

Fustec, J., Cormier, J.-P., & Lodé, T. (2003). Beaver lodge location on the upstream Loire River. *Comptes Rendus Biologies*, *326*, 192–199. https://doi.org/10.1016/S1631-0691(03)00057-X

Gable, T. (2021). *Wolf-Beaver Dynamics in a Southern Boreal Ecosystem*. http://conservancy.umn.edu/handle/11299/220607

Gable, T. D., Johnson-Bice, S. M., Homkes, A. T., Fieberg, J., & Bump, J. K. (2023). Wolves alter the trajectory of forests by shaping the central place foraging behaviour of an ecosystem engineer. *Proceedings of the Royal Society B: Biological Sciences*, *290*(2010), 20231377. https://doi.org/10.1098/rspb.2023.1377

Gable, T., & Windels, S. (2018). Kill rates and predation rates of wolves on beavers. *Journal of Wildlife Management*. https://doi.org/10.1002/jwmg.21387

Gable, T., Windels, S., Bruggink, J., & Homkes, A. (2016). Where and How Wolves (Canis lupus) Kill Beavers (Castor canadensis). *PLoS ONE*, *11*. https://doi.org/10.1371/journal.pone.0165537

Gable, T., Windels, S., Romanski, M., & Rosell, F. (2018). The forgotten prey of an iconic predator: A review of interactions between grey wolves Canis lupus and beavers Castor spp. *Mammal Review*, *48*, 123–138. https://doi.org/10.1111/mam.12118

Gaudi, S., Zoraqi, G., Falbo, V., & Taruscio, D. (2000). *Orologi biologici circadiani: Meccanismi molecolari autorigeneratori che mantengono il ritmo*. *36*(1), 99–109.

Gaywood, M. J. (2018). Reintroducing the Eurasian beaver Castor fiber to Scotland. *Mammal Review*, *48*(1), 48–61. https://doi.org/10.1111/mam.12113

Glacial lakes in the Šumava national park. (2019). https://www.czechia-tours.cz/post/glacial-lakes-in-the-%C5%A1umava-national-park

Gorner, T., Najmanova, K., & Cihar, M. (2012). Changes in Local People's Perceptions of the Sumava National Park in the Czech Republic over a Ten Year Period (1998–2008). *Sustainability*, *4*, 1354–1370. https://doi.org/10.3390/su4061354

Gwinner, E. (1996). Circannual clocks in avian reproduction and migration. *Ibis*, *138*(1), 47–63. https://doi.org/10.1111/j.1474-919X.1996.tb04312.x

Hall, G. (2020). *The Basics of Radio Telemetry*.

Halley, D. J., Saveljev, A. P., & Rosell, F. (2021). Population and distribution of beavers Castor fiber and Castor canadensis in Eurasia. *Mammal Review*, *51*(1), 1–24. https://doi.org/10.1111/mam.12216

Horníček, J., Šimůnková, K., Mokry, J., Korbelová, J., & Vorel, A. (2021). How Do the Beaver Home Ranges Vary during the Range Expansion? *Annales Zoologici Fennici*, *59*. https://doi.org/10.5735/086.059.0102

Hovardas, T. (A c. Di). (2018). *Large carnivore conservation and management: Human dimensions*. Routledge/Taylor and Francis Group.

Jačková, K., & Romportl, D. (2008). The Relationship Between Geodiversity and Habitat Richness in Šumava National Park and Křivoklátsko PLA (Czech Republic): A Quantitative Analysis Approach. *Journal of Landscape Ecology*, *1*(1), 23–38. https://doi.org/10.2478/v10285-012-0003-6

Janík, T. (2020). *Bavarian Forest and Šumava National Parks: On the way to transboundary wildlife management and conservation? 26*, 51–63.

Jędrzejewski, W., Niedzialkowska, M., Mysłajek, R. W., Nowak, S., & Jędrzejewska, B. (2005). Habitat selection by wolvesCanis lupus in the uplands and mountains of southern Poland. *Acta Theriologica*, *50*(3), 417–428. https://doi.org/10.1007/BF03192636

Jędrzejewski, W., Schmidt, K., Theuerkauf, J., Jędrzejewska, B., & Kowalczyk, R. (2007). Territory Size of Wolves Canis lupus: Linking Local (Białowieża Primeval Forest, Poland) and Holarctic-Scale Patterns. *Ecography*, *30*(1), 66–76.

Korbelová, J., Hamšíková, L., Maloň, J., Válková, L., & Vorel, A. (2016a). Seasonal variation in the home range size of the Eurasian beaver: Do patterns vary across habitats? *Mammal Research*, *61*. https://doi.org/10.1007/s13364-016-0265-1

Korbelová, J., Hamšíková, L., Maloň, J., Válková, L., & Vorel, A. (2016b). Seasonal variation in the home range size of the Eurasian beaver: Do patterns vary across habitats? *Mammal Research*, *61*(3), 243–253. https://doi.org/10.1007/s13364-016-0265-1

Křenová, Z., & Hruška, J. (2012). Proper zonation – an essential tool for the future conservation of the Šumava National Park. *European Journal of Environmental Sciences*, *2*(1), Articolo 1. https://doi.org/10.14712/23361964.2015.40

Krojerová-Prokešová, J., Barančeková, M., Hamšíková, L., & Vorel, A. (2010). Feeding habits of reintroduced Eurasian beaver: Spatial and seasonal variation in the use of food resources. *Journal of Zoology*, *281*, 183–193. https://doi.org/10.1111/j.1469-7998.2010.00695.x

Krzystek, P., Serebryanyk, A., Schnörr, C., Červenka, J., & Heurich, M. (2020). Large-Scale Mapping of Tree Species and Dead Trees in Šumava National Park and Bavarian Forest National Park Using Lidar and Multispectral Imagery. *Remote Sensing*, *12*(4), Articolo 4. https://doi.org/10.3390/rs12040661

Kusak, J., Skrbinšek, A. M., & Huber, D. (2005). Home ranges, movements, and activity of wolves (Canis lupus) in the Dalmatian part of Dinarids, Croatia. *European Journal of Wildlife Research*, *51*(4), 254–262. https://doi.org/10.1007/s10344-005-0111-2

Lancia, R. A., Dodge, W. E., & Larson, J. S. (1982). Winter Activity Patterns of Two Radio-Marked Beaver Colonies. *Journal of Mammalogy*, *63*(4), 598–606. https://doi.org/10.2307/1380264

Linkie, M., & Ridout, M. (2011). Assessing tiger-prey interactions in Sumatran rainforests. *Journal of Zoology*, *3*, 224–229. https://doi.org/10.1111/j.1469-7998.2011.00801.x

Lososová, J., Kouřilová, J., & Soukupová, N. (2021). Controversial approach to wolf management in the Czech Republic. *Agricultural Economics (Zemědělská ekonomika)*, *67*(No. 1), 1–10. https://doi.org/10.17221/377/2020-agricecon

Máca, O., Pavlásek, I., & Vorel, A. (2015). Stichorchis subtriquetrus (Digenea: Paramphistomatidae) from Eurasian beaver (Castor fiber) in the Czech Republic. *Parasitology Research*, *114*(8), 2933–2939. https://doi.org/10.1007/s00436-015-4495-y

MacNulty, D. R., Smith, D. W., Mech, L. D., Vucetich, J. A., & Packer, C. (2012). Nonlinear effects of group size on the success of wolves hunting elk. *Behavioral Ecology*, *23*(1), 75–82. https://doi.org/10.1093/beheco/arr159

Massolo, A., & Meriggi, A. (1998). Factors affecting habitat occupancy by wolves in northern Apennines (northern Italy): A model of habitat suitability. *Ecography*, *21*(2), 97–107. https://doi.org/10.1111/j.1600-0587.1998.tb00663.x

Mattioli, L., Apollonio, M., Mazzarone, V., & Centofanti, E. (1995). Wolf food habits and wild ungulate availability in the Foreste Casentinesi National Park, Italy. *Acta Theriologica*, *40*, 387–402. https://doi.org/10.4098/AT.arch.95-36

Mattioli, L., Capitani, C., Gazzola, A., Scandura, M., & Apollonio, M. (2011). Prey selection and dietary response by wolves in a high-density multi-species ungulate community. *European Journal of Wildlife Research*, *57*, 909–922. https://doi.org/10.1007/s10344-011-0503-4

Mech, L. D., Smith, D. W., & MacNulty, D. R. (2015). *Wolves on the Hunt: The Behavior of Wolves Hunting Wild Prey*. University of Chicago Press.

Meredith, M., & Ridout, M. (2018). *Overview of the overlap package*.

Meredith, M., Ridout, M., & Campbell, L. A. D. (2024). *Package 'overlap'—Estimates of Coefficient of Overlapping for Animal Activity Patterns*.

Mikulka, O., Pyszko, P., Kamler, J., Zdeněk, P., Jakub, D., Radim, P., Miloslav, H., & Jana, K. (2022a). Landscape settlement and parameters of Eurasian beaver (Castor fiber) home ranges in the Czech Republic. *European Journal of Wildlife Research*, *69*(1), 7. https://doi.org/10.1007/s10344-022-01624-4

Mikulka, O., Pyszko, P., Skoták, V., Kamler, J., Drimaj, J., Plhal, R., & Homolka, M. (2022b). The Influence of Forestry Management on the Selection of a Non-Vegetative Diet by the Eurasian Beaver (Castor fiber L.). *Animals*, *12*(21), Articolo 21. https://doi.org/10.3390/ani12212949

Mitchell, M., Powell, R., & Rachlow, J. (2012). Foraging optimally for home ranges. *Journal of Mammalogy*, *93*, 917–928. https://doi.org/10.2307/23259838

Mori, E., Mazza, G., Pucci, C., Senserini, D., Campbell-Palmer, R., Contaldo, M., & Viviano, A. (2022). Temporal Activity Patterns of the Eurasian Beaver and Coexisting Species in a Mediterranean Ecosystem. *Animals*, *12*(15), Articolo 15. https://doi.org/10.3390/ani12151961

Nelson, E. H., Matthews, C. E., & Rosenheim, J. A. (2004). Predators Reduce Prey Population Growth by Inducing Changes in Prey Behavior. *Ecology*, *85*(7), 1853–1858. https://doi.org/10.1890/03-3109

Newsome, T., Boitani, L., Chapron, G., Ciucci, P., Dickman, C., Dellinger, J., López-Bao, J. V., Peterson, R., Shores, C., Wirsing, A., & Ripple, W. (2016). Food habits of the world's grey wolves. *Mammal Review*, *46*, n/a-n/a. https://doi.org/10.1111/mam.12067

npsumava.cz. (s.d.). *Národní park Šumava*. Šumava National Park. Recuperato 26 agosto 2023, da https://www.npsumava.cz/en/

Oakleaf, J. K., Murray, D. L., Oakleaf, J. R., Bangs, E. E., Mack, C. M., Smith, D. W., Fontaine, J. A., Jimenez, M. D., Meier, T. J., & Niemeyer, C. C. (2006). Habitat Selection by Recolonizing Wolves in the Northern Rocky Mountains of the United States. *The Journal of Wildlife Management*, *70*(2), 554–563. https://doi.org/10.2193/0022-541X(2006)70[554:HSBRWI]2.0.CO;2

Oliveira, B., & Scheffers, B. (2018). Vertical stratification influences global patterns of biodiversity. *Ecography*, *42*. https://doi.org/10.1111/ecog.03636

Orrock, J., Dill, L., Sih, A., Grabowski, J., Peacor, S., Peckarsky, B., Preisser, E., Vonesh, J., & Werner, E. (2010). Predator Effects in Predator-Free Space: The Remote Effects of Predators on Prey. *Biological Sciences Faculty Publications*. https://doi.org/10.2174/1874213001003030022

Pachinger, K., & Hulik, T. (1999). Beavers in an Urban Landscape. In P. E. Busher & R. M. Dzięciołowski (A c. Di), *Beaver Protection, Management, and Utilization in Europe and North America* (pp. 53–60). Springer US. https://doi.org/10.1007/978-1-4615-4781-5_9

Packard, J. (2003). *Wolf behavior: Reproductive, social and intelligent* (pp. 35–65).

Padrtová, M. (2019). *Botanický průzkum nivy revitalizovaného úseku Jedlového potoka (NP Šumava)*. https://dspace.jcu.cz/handle/20.500.14390/41662

Peacor, S. D. (2002). Positive effect of predators on prey growth rate through induced modifications of prey behaviour. *Ecology Letters*, *5*(1), 77–85. https://doi.org/10.1046/j.1461-0248.2002.00287.x

Peinetti, H. R., Baker, B. W., & Coughenour, M. B. (2009). Simulation modeling to understand how selective foraging by beaver can drive the structure and function of a willow community. *Ecological Modelling*, *220*(7), 998–1012. https://doi.org/10.1016/j.ecolmodel.2009.01.009

Pittendrigh, C. S. (1960). Circadian rhythms and the circadian organization of living systems. *Cold Spring Harbor Symposia on Quantitative Biology*, *25*, 159–184. https://doi.org/10.1101/sqb.1960.025.01.015

Potvin, C. L., & Bovet, J. (1975). Annual cycle of patterns of activity rhythms in beaver colonies (Castor canadensis). *Journal of Comparative Physiology*, *98*(3), 243–256. https://doi.org/10.1007/BF00656972

Randler, C. (2006). Anti-predator response of Eurasian red squirrels (Sciurus vulgaris) to predator calls of tawny owls (Strix aluco). *Mammalian Biology*, *71*(5), 315–318. https://doi.org/10.1016/j.mambio.2006.02.006

Randler, C., & Kalb, J. (2020). Predator avoidance behavior of nocturnal and diurnal rodents. *Behavioural Processes*, *179*, 104214. https://doi.org/10.1016/j.beproc.2020.104214

Rehaume, J. (2023, marzo 8). Beavers and Riparian Habitats. *The Progressive Rancher*. https://progressiverancher.com/beavers-and-riparian-habitats/

Ridout, M., & Linkie, M. (2009). Estimating Overlap of Daily Activity Patterns From Camera Trap Data. *Journal of Agricultural Biological and Environmental Statistics*, *14*, 322–337. https://doi.org/10.1198/jabes.2009.08038

Roenneberg, T. (2012). *Internal Time: Chronotypes, Social Jet Lag, and Why You're So Tired*. https://doi.org/10.4159/harvard.9780674065482.intro

Roenneberg, T., & Merrow, M. (2005). Circadian clocks—The fall and rise of physiology. *Nature Reviews Molecular Cell Biology*, *6*(12), Articolo 12. https://doi.org/10.1038/nrm1766

Rosell, F., & Czech, A. (2000). Response of foraging Eurasian beavers Castor fiber to predator odours. *Wildlife Biology*, *6*. https://doi.org/10.2981/wlb.2000.033

Rosell, F., & Sanda, J. (2006). Potential risks of olfactory signaling: The effect of predators on scent marking by beavers. *Behavioral Ecology*, *17*, 897–904. https://doi.org/10.1093/beheco/arl022

Rothmeyer, S. W., McKinstry, M. C., & Anderson, S. H. (2002). Tail Attachment of Modified Ear-Tag Radio Transmitters on Beavers. *Wildlife Society Bulletin (1973-2006)*, *30*(2), 425–429.

Sánchez-Ferrer, J. C., Servín, J., Muñoz-Delgado, J., Murata, C., Méndez Ramírenz, I., Sánchez-Robles, J., & López-Wilchis, R. (2016). Variations in the locomotor activity of the Mexican wolf (Canis lupus baileyi) respect to moon periodicity: A study in an outdoor enclosure. *Biological Rhythm Research*, *47*(4), 539–551. https://doi.org/10.1080/09291016.2016.1164281

Schenkel, R. (1967). Submission: Its Features and Function in the Wolf and Dog. *American Zoologist*, *7*(2), 319–329.

Scherzinger, W. (2005). *Wolf occurrence in the Czech-Bavarian-Austrian border region—Review of the history and current status*. https://www.academia.edu/65652132/Wolf_occurrence_in_the_Czech_Bavarian_Austrian_border_region_review_of_the_history_and_current_status

Selmy.cz, FoS CU, & FES CULS. (2022, febbraio 11). *The annual wolf monitoring confirms two new wolf territories in the Czech Republic*. Carnivores.cz. http://www.carnivores.cz/press-news/the-annual-wolf-monitoring-confirms-two-new-wolf-territories-in-the-czech-republic/

Severud, W., Belant, J., Bruggink, J., & Windels, S. (2011). Predator Cues Reduce American Beaver Use of Foraging Trails. *Human-Wildl. Interac.*, *5*. https://doi.org/10.26077/n3q0-7352

Sharma, V. (2003). Adaptive Significance of Circadian Clocks. *Chronobiology international*, *20*, 901–919. https://doi.org/10.1081/CBI-120026099

Stych, P., Lastovicka, J., Hladky, R., & Paluba, D. (2019). Evaluation of the Influence of Disturbances on Forest Vegetation Using the Time Series of Landsat Data: A Comparison Study of the Low Tatras and Sumava National Parks. *ISPRS International Journal of Geo-Information*, *8*(2), Articolo 2. https://doi.org/10.3390/ijgi8020071

Šumava National Park. (s.d.). Amazing Czechia. Recuperato 27 agosto 2023, da https://www.amazingczechia.com/destinations/sumava-national-park/

Svoboda, M., Fraver, S., Janda, P., Bače, R., & Zenáhlíková, J. (2010). Natural development and regeneration of a Central European montane spruce forest. *Forest Ecology and Management*, *260*(5), 707–714. https://doi.org/10.1016/j.foreco.2010.05.027

Swinnen, K. R. R., Hughes, N. K., & Leirs, H. (2015). Beaver (Castor fiber) activity patterns in a predator-free landscape. What is keeping them in the dark? *Mammalian Biology*, *80*(6), 477–483. https://doi.org/10.1016/j.mambio.2015.07.006

Taylor, J., Yarrow, G., & Miller, J. (2017). *Beavers*.

Treves, A., Bottero, M., Caprioli, C., & Comino, E. (2020). The reintroduction of Castor fiber in Piedmont (Italy): An integrated SWOT-spatial multicriteria based approach for the analysis of suitability scenarios. *Ecological Indicators*, *118*, 106748. https://doi.org/10.1016/j.ecolind.2020.106748

Uhlíková, J. (2016). *Odlov bobrů v jižních Čechách*. https://www.myslivost.cz/Casopis-Myslivost/Myslivost/2016/Cervenec-2016/ODLOV-BOBRU-V-JIZNICH-CECHACH

van den Bosch, M., Kellner, K. F., Gantchoff, M. G., Patterson, B. R., Barber-Meyer, S. M., Beyer, D. E., Erb, J. D., Isaac, E. J., MacFarland, D. M., Moore, S. A., Norton, D. C., Petroelje, T. R., Price Tack, J. L., Roell, B. J., Schrage, M., & Belant, J. L. (2023). Habitat selection of resident and non-resident gray wolves: Implications for habitat connectivity. *Scientific Reports*, *13*(1), Articolo 1. https://doi.org/10.1038/s41598-023-47815-0

Vitaterna, M. H., Takahashi, J. S., & Turek, F. W. (2001). Overview of Circadian Rhythms. *Alcohol Research & Health*, *25*(2), 85–93.

Vorel, A., Dostál, T., Uhlíková, J., Korbelová, J., & Koudelka, P. (2017). *Handbook for Coexisting with Beavers CZE*.

Vorel, A., Kadlec, I., Toulec, T., Selimovic, A., Horníček, J., Vojtěch, O., Mokrý, J., Pavlačík, L., Arnold, W., Cornils, J., Kutal, M., Duľa, M., Žák, L., & Bartak, V. (2023). *Home range analysis and habitat preferences of wolves recolonising Central European human-dominated landscapes* [Preprint]. Preprints. https://doi.org/10.22541/au.169781252.26180018/v1

Vorel, A., Mokry, J., & Šimůnková, K. (2014). The population growth of Eurasian beaver in the Bohemian Forest. *Silva Gabreta*, *20*, 25–40.

Vorel, A., Šafář, J., & Šimůnková, K. (2012). Recent expansion of Castor fiber in the Czech Republic during 2002–2012 (Rodentia: Castoridae). *Lynx*, *43*, 149–179.

Vorel, A., Válková, L., Ham, L., Malo, J., & Korbelová, J. (2008). *THE EURASIAN BEAVER POPULATION MONITORING STATUS IN THE CZECH REPUBLIC*. *17*.

Vorel, A., Válková, L., Hamšíková, L., Maloň, J., & Korbelová, J. (2015). Beaver foraging behaviour: Seasonal foraging specialization by a choosy generalist herbivore. *Behavioral Ecology and Sociobiology*, *69*, 1221–1235. https://doi.org/10.1007/s00265-015-1936-7

Vos, J. (2000). Food habits and livestock depredation of two Iberian wolf packs (Canis lupus signatus) in the north of Portugal. *Journal of Zoology*, *251*(4), 457–462. https://doi.org/10.1111/j.1469-7998.2000.tb00801.x

Whittington, J., St. Clair, C. C., & Mercer, G. (2005). Spatial Responses of Wolves to Roads and Trails in Mountain Valleys. *Ecological Applications*, *15*(2), 543–553. https://doi.org/10.1890/03-5317

Zimmermann, B. (2014). *Predatory behaviour of wolves in Scandinavia* [Doctoral thesis]. https://brage.inn.no/inn-xmlui/handle/11250/194207

Zýval, V., Křenová, Z., & Kindlmann, P. (2016). Conservation implications of forest changes caused by bark beetle management in the Šumava National Park. *Biological Conservation*, *204*, 394–402. https://doi.org/10.1016/j.biocon.2016.11.001